

# LOWER CARBONIFEROUS MICROFLORAS OF SPITSBERGEN

by G. PLAYFORD

## PART TWO

Part I of this paper will be found in Volume 5, Part 3, pages 550–618, with an abstract on page 550; it includes the list of references. Part II continues and concludes the paper; a contents list is placed at the end of this part.

### *Anulatisporites orbiculatus* (Waltz) comb. nov.

Plate 88, fig. 1

1941 *Zonotriletes orbiculatus* Waltz in Lubert and Waltz, p. 24; pl. 4, fig. 60.

1957 *Euryzonotriletes orbiculatus* (Waltz) Naumova; Kedo, p. 1168.

*Diagnosis.* The following is the present writer's translation of the diagnosis given by Waltz (in Lubert and Waltz 1941, p. 24): 'Diameter—92·5–137·5  $\mu$ . Colour brownish yellow. Spore body outline circular; surface of body smooth. Border wide, rather thick, with even or slightly fluted outer edge. On surface of border small wrinkles or folds having concentric orientation are sometimes observed. Thickness of exine on spore body and on border approximately equal. Trilete fissures very prominent, smooth, equal, slightly elevated or thickened. Length of rays equal to, or slightly less than, spore body radius. *Z. orbiculatus* Waltz is characterized by a considerable variation in the ratio between diameter of spore body and width of border. Diameter of spore body 50–70  $\mu$ . Width of border 15–75  $\mu$ .'

*Description of specimens.* The Spitsbergen specimens conform closely to the above diagnosis. Exine thickness is 2·5–4  $\mu$  on spore body. Cingulum of any particular specimen is of uniform width. Surface of cingulum laevigate to infrapunctate (oil immersion); punctate in corroded specimens, particularly around spore-body margin.

*Dimensions* (12 specimens). Overall equatorial diameter 92–120  $\mu$  (mean 105  $\mu$ ); diameter of spore body 49–71  $\mu$  (mean 61  $\mu$ ); width of cingulum 16–30  $\mu$  (mean 22  $\mu$ ).

*Remarks.* The species is included in the genus *Anulatisporites* on the basis of its broad, sculptureless cingulum.

*Previous records.* *Anulatisporites orbiculatus* (Waltz) comb. nov. has been recorded from Tournaisian–Viséan strata of the Kizel district, U.S.S.R. (Lubert and Waltz 1941), and from the Viséan of White Russia (Kedo 1957, 1958, 1959).

### *Anulatisporites canaliculatus* sp. nov.

Plate 88, figs. 2, 3

*Diagnosis.* Spores radial, trilete; amb smooth, subtriangular with well-rounded apices and convex sides. Laesurae distinct, straight, length approximately 1·5–4  $\mu$  less than [Palaeontology, Vol. 5, Part 4, 1962, pp. 619–678, pls. 88–95.]

spore-body radius; accompanied by conspicuous, flat, smooth, slightly elevated lips, which extend  $4-7\ \mu$  on either side of laesurae and often have lobed outer margins. Spore body laevigate. Cingulum distinctively incised on proximal surface by a single, continuous, very narrow furrow situated approximately  $2.5-5.5\ \mu$  from, and more or less conformable with, smooth spore-body margin. Cingulum otherwise undifferentiated, laevigate (irregularly punctate in corroded specimens), uniformly broad, much darker in colour than spore body.

*Dimensions* (35 specimens). Overall equatorial diameter  $54-86\ \mu$  (mean  $70\ \mu$ ); diameter of spore body  $33-50\ \mu$  (mean  $41\ \mu$ ); width of cingulum  $11-21\ \mu$  (mean  $15\ \mu$ ).

*Holotype*. Preparation P173/2, 53.1 100.1. L.1125.

*Locus typicus*. Citadellet (sample G1446), Spitsbergen; Lower Carboniferous.

*Description*. Holotype  $79\ \mu$  overall, spore-body diameter  $45\ \mu$ , width of cingulum  $17\ \mu$ ; laesurae extending to within  $2.5\ \mu$  of spore-body margin, lips individually about  $4.5\ \mu$  wide; furrow incised in cingulum uniformly about  $4\ \mu$  from spore-body margin, depth about  $2\ \mu$ . In some specimens the margin between the spore body and the cingulum on the distal hemisphere may be rather undulating showing only general conformity to equatorial outline.

*Comparison*. The generally larger *Zonotriletes sulcatus* Waltz (in Lubert and Waltz 1938, p. 18; pl. 2, fig. 20) has numerous, rather discontinuous, concentric furrows in the cingulum, which is definitely thickened at its inner margin.

#### Genus DENSOSPORITES (Berry) Potonié and Kremp 1954

*Type species*. *D. covensis* Berry 1937.

*Discussion*. This genus and the morphographically associated *Anulatisporites* Loose ex Potonié and Kremp 1954 are presently receiving consideration from a subcommittee of the International Commission for the Microflora of the Palaeozoic; as a result, their redefinition, together with the erection of several other related genera, seems likely. This reappraisal of the densospore group will be based principally upon the sculpture of the cingulum, and it is to be hoped that due regard will be given to the effects of corrosion, both natural and in preparation, which in many cases seems to cause profound cingulate alteration (cf. Bharadwaj 1959, p. 70). Pending publication of the Commission's proposals, the Spitsbergen spores concerned are here assigned to either *Densosporites* or to *Anulatisporites* as formally emended by Potonié and Kremp (1954).

*Affinity*. In view of the abundance of representatives of this genus in sediments (particularly coals) of Carboniferous age, it is surprising that only recently has evidence come forward as to its botanical affinity. Chaloner (1958a) reported microspores similar to *Densosporites loricatus* (Loose) Schopf, Wilson, and Bentall 1944 from a small Upper Carboniferous lycopod cone compression, which he termed *Selaginellites canonbiensis* sp. nov. Subsequently, Bharadwaj (1959) obtained microspores conformable with *Densosporites* from the heterosporous lycopod strobilus *Porostrobus zeilleri* Nathorst 1914 which had been collected from Lower Carboniferous strata at Pyramiden, Spitsbergen. It will be seen that the abundantly occurring *spora dispersae*, described below as *Densosporites spitsbergensis* sp. nov., resemble closely the microspores obtained by

Bharadwaj (from *P. zeilleri*). In a postscript to his paper, Bharadwaj recommended the inclusion of *Selaginellites canonbiensis* Chaloner within *Bothrostrobus* (Nathorst) Seward.

*Densosporites bialatus* (Waltz) Potonié and Kremp 1956

Plate 88, figs. 4–7

- 1938 *Zonotriletes bialatus* Waltz in Lubert and Waltz, p. 22; pl. 4, fig. 51.  
1941 *Zonotriletes bialatus* Waltz var. *undulatus* Waltz in Lubert and Waltz, pp. 28–29; pl. 5, fig. 71a, b.  
1941 *Zonotriletes bialatus* Waltz var. *costatus* Waltz in Lubert and Waltz, p. 29; pl. 5, fig. 72.  
1952 *Hymenozonotriletes* aff. *bialatus* (Waltz) Ishchenko, p. 51; pl. 13, fig. 124.  
1956 *Densosporites bialatus* (Waltz) Potonié and Kremp, p. 114.  
1956 *Hymenozonotriletes bialatus* (Waltz) var. *undulatus* (Waltz) Ishchenko, pp. 63–64; pl. 12, figs. 135–7.  
1957 *Cingulizonates tuberosus* Dybová and Jachowicz, p. 171; pl. 53, figs. 1–4.  
1957 *Trematozonotriletes bialatus* (Waltz) Naumova; Byvsheva, p. 1010.

*Description of specimens.* Spores radial, trilete; amb roundly subtriangular to oval, more or less conformable with convexly subtriangular body outline. Laesurae perceptible or not visible (corroded specimens); simple, straight to sinuous, length approximately equal to body radius. Where preserved, body exine is finely granulate or punctate. Differentiated cingulum, consisting of: an inner, thickened, opaque portion characteristically sculptured with fine, radially elongated pits; surrounded by a thinner, translucent zone which is approximately one-third to half of the total cingulum width. Conspicuous junction between the two parts of the cingulum may be regular, conforming closely with the spore-body outline; in many cases, however, it is irregularly lobed or dentate due to radial, equatorially tapering extensions of the thickened part projecting into, but rarely attaining margin of, the outer thinner portion.

*Dimensions* (60 specimens). Overall equatorial diameter 46–77  $\mu$  (mean 60  $\mu$ ); diameter of spore body 21–34  $\mu$  (mean 27  $\mu$ ).

*Remarks.* In her diagnosis of *Zonotriletes bialatus*, Waltz (in Lubert and Waltz 1938, p. 22) drew attention to the variable structure of the inner thickened portion of the cingulum, suggesting its dependence upon the state of preservation. Subsequently, Waltz (in Lubert and Waltz 1941, pp. 28–29) delineated two varieties (*undulatus* and *costatus*) within the species, on the basis of this variation. Both varieties are represented in the Spitsbergen assemblages, but their continuous intergradation does not support their recognition as separate morphographical units. The illustrations of *Cingulizonates tuberosus* Dybová and Jachowicz 1957 (pl. 53, figs. 1–4) strongly suggest conspecificity with *Densosporites bialatus* (Waltz), and indeed Jachowicz (1958, table 8) subsequently equated the two species.

There seems little doubt of the presence of *D. bialatus* within the Upper Mississippian spore assemblage described by Hacquebard and Barss (1957). These authors remarked (p. 32) that their species *Densosporites irregularis* 'may be conspecific with *Zonotriletes bialatus* Waltz, 1938', and certainly the spores represented by their plate 4, figs. 12, 13 (*D. irregularis*) and by plate 4, fig. 10 (*D. cuneiformis*) show close resemblance to *D. bialatus*.

*Previous records.* *Densosporites bialatus* (Waltz) has been recorded by numerous Russian



palynologists from the Lower Carboniferous of the U.S.S.R. (Luber and Waltz 1938, 1941; Ishchenko 1952, 1956, 1958; Byvsheva 1957, 1960; Loginova 1959). It has been recorded also from the Namurian A to Westphalian B interval of the Upper Silesian Coal Measures (Dybová and Jachowicz 1957; Jachowicz 1958), and is probably present in the Upper Mississippian of the South Nahanni River area, Northwest Territories, Canada (Hacquebard and Barss 1957).

Ishchenko (1956) documented occurrences of the species, in the western Donetz Basin, from Viséan to Namurian, and subsequently (1958), in the Dnieper-Donetz Basin, from Tournaisian to Bashkirian.

*Densosporites dentatus* (Waltz) Potonié and Kremp 1956

Plate 88, figs. 14, 15

1884 Type 274 of Reinsch, p. 27; pl. 20, fig. 128A.

1938 *Zonotriletes dentatus* Waltz in Luber and Waltz, p. 20; pl. 14, fig. 47.

1956 *Densosporites dentatus* (Waltz) Potonié and Kremp, p. 115.

1958 *Hymenozonotriletes dentatus* (Waltz) Ishchenko, pp. 70-71; pl. 7, fig. 96.

*Description of specimens.* Spores radial, trilete; amb oval to roundly subtriangular. Laesurae simple, straight to sinuous, extending to spore-body margin. Exine of spore body laevigate to granulate; very thin, hence often poorly preserved or absent. Cingulum uniform, relatively dark in colour, width 9-20  $\mu$ , equatorial margin regularly dentate.

*Dimensions* (50 specimens). Overall equatorial diameter 36-65  $\mu$  (mean 49  $\mu$ ); diameter of spore body 20-31  $\mu$  (mean 25  $\mu$ ).

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EXPLANATION OF PLATE 88

All figures  $\times 500$ , and from unretouched negatives.

Fig. 1. *Anulatisporites orbiculatus* (Waltz) comb. nov. Proximal surface; preparation P148/4, 48.2 95.0 (L.1124).

Figs. 2, 3. *Anulatisporites canaliculatus* sp. nov. 2, Proximal surface; preparation P163/6, 44.2 112.7 (L.1126). 3, Holotype; proximal surface.

Figs. 4-7. *Densosporites bialatus* (Waltz) Potonié and Kremp 1956. 4, Distal surface; preparation P164/5, 38.2 93.1 (L.1129). 5, Distal surface; preparation P164/9, 35.3 101.4 (L.1128). 6, Proximal surface; preparation P167B/3, 50.6 95.1 (L.1130). 7, Distal surface; preparation P167B/1, 28.6 94.3 (L.1131).

Figs. 8, 9. *Densosporites subcrenatus* (Waltz) Potonié and Kremp 1956. 8, Proximal surface; preparation P145B/32, 41.5 103.3 (L.1134). 9, Proximal surface; preparation P145C/1, 29.0 94.9 (L.1135).

Figs. 10, 11. *Densosporites diatretus* nom. nov. 10, Proximal surface; preparation P176A/1, 40.9 95.4 (L.1137). 11, Distal surface; preparation P148/1, 25.0 95.4 (L.1136).

Figs. 12, 13. *Densosporites striatiferus* Hughes and Playford 1961. 12, Proximal surface; preparation P172/3, 25.9 95.5 (L.1145). 13, Proximal surface; preparation P170/1, 23.8 97.2 (L.1144).

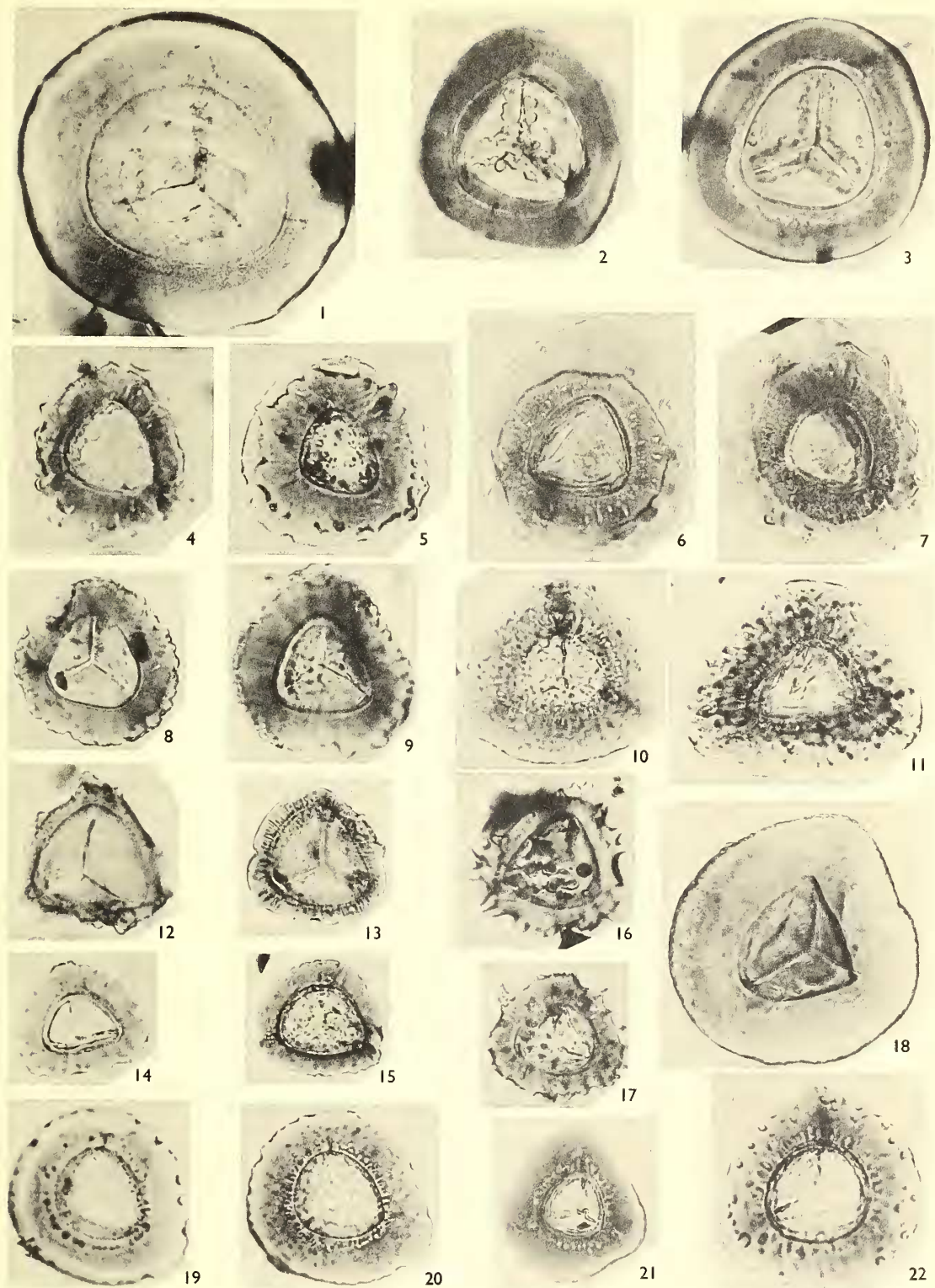
Figs. 14, 15. *Densosporites dentatus* (Waltz) Potonié and Kremp 1956. 14, Proximal surface; preparation P148/1, 45.2 95.6 (L.1132). 15, Distal surface; preparation P143B/5, 33.8 106.7 (L.1133).

Figs. 16, 17. *Densosporites aculeatus* sp. nov. 16, Holotype; distal surface. 17, Proximal surface; preparation P201/2, 29.8 102.1 (L.1164).

Fig. 18. *Densosporites* sp. Proximal surface; preparation P167B/13, 38.8 103.0 (L.1166).

Figs. 19-22. *Densosporites variabilis* (Waltz) Potonié and Kremp 1956. 19, 20, Distal and proximal surfaces respectively; preparation P154/6, 22.7 100.8 (L.1140). 21, Proximal surface; preparation P145B/31, 36.3 102.7 (L.1138). 22, Proximal surface; preparation P158/4, 21.1 93.5 (L.1139).





PLAYFORD, Lower Carboniferous microspores



*Comparison.* Some of the spores described by Hoffmeister, Staplin, and Malloy (1955, p. 386; pl. 36, figs. 16, 17) as *Densosporites spinifer*, and subsequently recorded as such by Butterworth and Williams (1958, p. 359; pl. 3, fig. 46) and by Love (1960, p. 109), may be representative of *D. dentatus* (Waltz).

*Previous records.* Recorded initially by Reinsch (1884) from the Russian Carboniferous. Later and more precisely documented Russian occurrences are from the Lower Carboniferous of the Moscow Basin and of the Kizel, Selizharovo, Voronezh, and Borovichi districts (Luber and Waltz 1938, 1941), and from exclusively Viséan sediments of the Dnieper–Donetz Basin (Ishchenko 1958). Thus this Spitsbergen occurrence is the first reported definitely outside Russia.

*Densosporites subcrenatus* (Waltz) Potonié and Kremp 1956

Plate 88, figs. 8, 9

1938 *Zonotriletes subcrenatus* Waltz in Luber and Waltz, p. 19; pl. 4, fig. 43.

1956 *Densosporites subcrenatus* (Waltz) Potonié and Kremp, p. 116.

1958 *Hymenozonotriletes subcrenatus* (Waltz) Ishchenko, p. 77; pl. 9, fig. 112.

[non *Tendosporites subcrenatus* (Waltz) Hacquebard and Barss 1957, p. 36; pl. 5, figs. 3, 4.]

*Description of specimens.* Spores radial, trilete; amb subtriangular, more or less conformable with spore-body outline. Laesurae distinct, simple, straight, length slightly less than body radius. Spore-body exine essentially laevigate, sometimes finely wrinkled; body outline triangular with rounded apices and  $\pm$  straight sides. Cingulum laevigate; with crenulate, fringe-like equatorial margin which is often at least partially absent in poorly preserved specimens. Corroded specimens often tend to approach the aspect of *Tripartites*, notably of *T. incisotrilobus* (Naumova; Waltz) Potonié and Kremp 1956 (cf. Waltz in Luber and Waltz 1938, p. 19; Ishchenko 1958, p. 77), although incisement or embayment of the cingulum is not necessarily located interradially.

*Dimensions* (30 specimens). Overall equatorial diameter 44–65  $\mu$  (mean 55  $\mu$ ); diameter of spore body 26–39  $\mu$  (mean 32  $\mu$ ).

*Comparison.* The specimens described by Hacquebard and Barss (1957, p. 36; pl. 5, figs. 3, 4) as *Tendosporites subcrenatus* (Waltz) were incorrectly referred to Waltz's species, since they possess a cingulum which is 'irregularly thickened at the periphery'; this is not a feature diagnosed by Waltz or evident from the Spitsbergen representatives. Some of the spores figured by Reinsch (1884, e.g. pl. 3, figs. 38, 41; pl. 17, fig. 41; pl. 19, fig. 41D; pl. 20, fig. 118L) resemble *Densosporites subcrenatus* (Waltz).

*Previous records.* Previous definite occurrences are confined to the Russian Lower Carboniferous. Luber and Waltz (1938, 1941) record the species from the Moscow Basin and Kizel region, and Ishchenko (1958, stratigraphical range table 3) found it to be restricted to Viséan–Namurian strata of the Dnieper–Donetz Basin.

*Densosporites diatretus* nom. nov.

Plate 88, figs. 10, 11; text-fig. 9a

1941 *Zonotriletes intermedius* Waltz in Luber and Waltz, pp. 27–28; pl. 5, fig. 68.

1956 *Hymenozonotriletes intermedius* (Waltz) Ishchenko, pp. 64–65; pl. 12, fig. 139.

[non *Densosporites intermedius* Butterworth and Williams, 1958, p. 379; pl. 3, figs. 38, 39.]



*Diagnosis.* The following is the present writer's translation of the diagnosis given by Waltz (*in* Lubert and Waltz 1941): 'Diameter—55–70  $\mu$ . Colour brownish yellow. Outline of spore body roundly triangular. Border wide, thick, bearing superficially two types of sculpture. Nearer to the inside edge of the border is an arrangement of short, radial grooves; on the rest of the surface sparsely distributed tuberculate thickenings can be observed. The former type of sculpture comes close to that of *Zonotriletes variabilis* Waltz var. *valleculosus* Waltz, the second shows much similarity to the sculpture of *Zonotriletes polyzonalis* Waltz. The fact that the species described is found in conjunction with the two others mentioned, and also the similarity of morphological features, argues in favour of the existence of a definite link between them. Diameter of spore body 15–25  $\mu$ . Width of border 15–30  $\mu$ .'

*Holotype* (here designated). Spore illustrated by Lubert and Waltz 1941, pl. 5, fig. 68 (here reproduced as Text-fig. 9a).



TEXT-FIG. 9. a, *Densosporites diatretus* nom. nov., redrawn from Lubert and Waltz 1941, pl. 5, fig. 68. b, *Lophozonotriletes rarituberculatus* (Lubert) Kedo 1957, redrawn from Lubert and Waltz 1941, pl. 5, fig. 76. c.  $\times 500$ .

*Description of specimens.* Those observed in the Spitsbergen assemblages conform closely to the above diagnosis, and to the following additional remarks.

Amb varies from convexly subtriangular to triangular (this variation was noted also by Ishchenko 1956, 1958). The radial grooves are confined to the inner margin of the proximal surface of the cingulum, and are often much finer and more closely spaced than in the spore illustrated by Waltz (*in* Lubert and Waltz 1941; pl. 5, fig. 68) and reproduced herein (text-fig. 9a). The positive sculptural elements on the remainder of the cingulum are usually more strongly developed on the distal surface; in different specimens they range from small conical to larger rod-like thickenings. The cingulum is often rather indistinctly differentiated into an outer light zone and an inner, darker (thicker) zone; this feature was emphasized by Ishchenko (1958, p. 71). Laesurae, apparent only on well-preserved specimens, are distinct, simple, straight to slightly sinuous, length approximately equal to spore-body radius, sometimes extending on to cingulum.

*Dimensions* (70 specimens). Overall equatorial diameter 55–76  $\mu$  (mean 66  $\mu$ ); diameter of spore body 16–35  $\mu$  (mean 25  $\mu$ ); width of cingulum 14–25  $\mu$  (mean 20  $\mu$ ).

*Remarks.* This species is included within *Densosporites* (Berry) Potonié and Kremp on the basis of its massive, distinctively sculptured cingulum. Ishchenko (1956, 1958) transferred *Zonotriletes intermedius* Waltz 1941 to *Hymenozonotriletes* Naumova 1937; however, the latter genus as understood by Potonié (1958, p. 29) and evidently by

Naumova (1953) embraces prominently zonate forms having conspicuous spinose sculpture. Thus Ishchenko's assignment of this species is unacceptable.

*Comparison.* *Densosporites diatretus* nom. nov. shows some resemblance to *Vallatisporites* Hacquebard (1957, p. 312) but lacks the distinct 'groove or rampart-like area' characteristic of that genus. Butterworth and Williams (1958, p. 379) described, from the Scottish Lower Carboniferous, a species which they named *Densosporites intermedius*. These spores are clearly different from those of *Hymenozonotriletes intermedius* (Waltz 1941); hence it is necessary to erect a new trivial epithet for the species on its inclusion in *Densosporites* (ref. articles 55 and 64 of the 1961 International Code of Botanical nomenclature).

*Previous records.* *Densosporites diatretus* nom. nov. has been recorded previously from Russia only, as follows: Lower Carboniferous of the Moscow Basin and Kizel region (Luber and Waltz 1941); Tournaisian to Middle Viséan only of the western extension of the Donetz Basin (Ishchenko 1956); and Tournaisian, Viséan, and Namurian of the Dnieper-Donetz Basin (Ishchenko 1958).

*Densosporites variabilis* (Waltz) Potonié and Kremp 1956

Plate 88, figs. 19-22

- 1938 *Zonotriletes variabilis* Waltz in Luber and Waltz, pp. 20-21; pl. 4, figs. 44-46, and pl. A, fig. 16.  
1941 *Zonotriletes variabilis* Waltz var. *foveolatus* Waltz in Luber and Waltz, p. 26; pl. 5, fig. 66a.  
1941 *Zonotriletes variabilis* Waltz var. *fossulatus* Waltz in Luber and Waltz, p. 26; pl. 5, fig. 66b.  
1941 *Zonotriletes variabilis* Waltz var. *valleculosus* Waltz in Luber and Waltz, p. 27; pl. 5, fig. 66c.  
1956 *Densosporites variabilis* (Waltz) Potonié and Kremp, p. 116.  
1956 *Trematozonotriletes variabilis* (Waltz) Ishchenko var. *foveolatus* Waltz; Ishchenko, pp. 102-3; pl. 22, fig. 248.  
1957 *Trematozonotriletes variabilis* (Waltz) Naumova; Byvsheva, p. 1010.  
[non *Densosporites variabilis* (Waltz) Potonié and Kremp; Butterworth and Williams 1958, pp. 380-1; pl. 3, figs. 32-34.]

*Description of specimens.* Spores radial, trilete; amb roundly subtriangular. Laesurae straight to sinuous, elevated and slightly thickened; frequently not preserved due to delicate spore-body exine. Uniformly thick cingulum prominently sculptured on proximal surface with numerous shallow pits or grooves arranged radially around outer margin of spore body; cavities rarely extend radially beyond centre of cingulum. Additional, irregular pitting on cingulum is often present, and may be attributable to corrosion. Spore body laevigate to granulate; outline more or less conformable with amb. Equatorial margin smooth, undulating, dentate or lobate.

*Dimensions* (80 specimens). Overall equatorial diameter 41-77  $\mu$  (mean 60  $\mu$ ); diameter of spore body 19-34  $\mu$  (mean 26  $\mu$ ).

*Remarks.* Three of the four illustrations of *Zonotriletes variabilis* in Luber and Waltz 1938 (pl. 4, figs. 44-46) were reproduced in Luber and Waltz 1941 (pl. 5, fig. 66a-c) and designated infraspecifically as the following varieties: *foveolatus*, *fossulatus*, and *valleculosus*, respectively. However, continuous morphographical variation between these forms

was noted by Waltz and is confirmed abundantly in the present investigation; as such, their infraspecific recognition does not appear warranted.

*Comparison.* *Densosporites diatretus* resembles *D. variabilis* (Waltz) in possessing similarly disposed radial grooves in the cingulum, which, however, is sculptured additionally with conspicuous tuberculate thickenings. As noted by Waltz (*in* Lubert and Waltz 1941), *D. diatretus* represents a sculptural intermediate between *D. variabilis* and *D. polyzonalis* (Waltz) Potonié and Kremp 1956. In the Spitsbergen assemblages the former two species are commonly although not invariably associated, and are certainly at least morphologically closely related. However, specimens positively identifiable with *D. polyzonalis* have not been observed by the writer.

Although showing similar sculpture to the specimens described above, *Trematizonotriteles variabilis* (Waltz) var. *trigonalis* Ishchenko 1956 (p. 103; pl. 20, fig. 249) possesses a cingulum which is consistently wider about the spore apices, and as such probably represents a distinct species.

Butterworth and Williams (1958) incorrectly assigned to *Densosporites variabilis* (Waltz) a species which they described as being 'abundant throughout' their Scottish Namurian assemblages; these authors implied identity of their specimens with that illustrated by Lubert and Waltz 1938 (pl. 4, fig. 46, subsequently *Zonotriteles variabilis* Waltz var. *valleculosus* Waltz 1941). However, from the description and photographs given by Butterworth and Williams (1958, pp. 380–1; pl. 3, figs. 32–34) and from the study of a slide kindly loaned to the writer by Dr. Butterworth, it is clear that the Scottish specimens differ from *D. variabilis* in the following important respects: (1) the spore body is rather poorly defined; (2) the cingulum shows relatively abrupt equatorial reduction in thickness; (3) the cingulate sculpture consists of irregular, elevated, radial thickenings enclosing equally irregular, and not invariably radially disposed, lumina, which are often imperfectly defined and are not concentrated along the inner margin of the cingulum. In contrast, *D. variabilis* possesses closely spaced, well-defined, pyriform pits, which are radially arranged about the distinct spore body, sharply punctuating an otherwise featureless cingulum of fairly uniform thickness; there is no appearance of the 'radial struts' described by Butterworth and Williams.

*Previous records.* *Densosporites variabilis* has been reported by numerous authors (Lubert and Waltz 1938, 1941; Ishchenko 1956, 1958; Bludorov and Tuzova 1956; Byvsheva 1957; Kedo 1957, 1958, 1959; Loginova 1959) as an important constituent of Tournaisian, and particularly Viséan–Namurian strata in the U.S.S.R. Recently Love (1960) recorded the species from the Pumpherston Shell Bed (Viséan) of Scotland, and Hughes and Playford (1961) reported its predominance in one sample (S59a) of the Spitsbergen Lower Carboniferous.

*Densosporites duplicatus* (Naumova) Potonié and Kremp 1956

Plate 89, figs. 6–8

1884 Type 336 of Reinsch, p. 33; pl. 16, fig. 125A.

1884 Type 337 of Reinsch, p. 33; pl. 9, fig. 125.

1938 *Zonotriteles duplicatus* (Naumova) Waltz *in* Lubert and Waltz, p. 21; pl. 4, fig. 53.

1956 *Densosporites duplicatus* (Naumova) Potonié and Kremp, p. 115.

1957 *Labiadensites* cf. *Z. duplicatus* (Naumova; Waltz) Hacquebard and Barss, p. 27; pl. 6, fig. 1.



*Description of specimens.* Spores radial, trilete; amb roundly subtriangular to sub-circular. Laesurae distinct, straight, length equal to, or slightly less than, spore-body radius; usually accompanied by minor lip development—lips individually about  $3\ \mu$  broad, with somewhat irregular outer margins. Spore body concavely or convexly subtriangular to subcircular; laevigate to finely granulate. Outer margin of cingulum strongly and characteristically differentiated into numerous laterally projecting processes which are approximately  $10\text{--}15\ \mu$  long,  $3\text{--}4\ \mu$  in basal diameter, and are conspicuously expanded and thickened apically into crescentic (mushroom-shaped) caps. These prominent peltate processes are usually very closely packed, often appearing to lie in more than one horizontal plane. Cingulum otherwise laevigate, colour slightly darker than body.

*Dimensions* (70 specimens). Overall equatorial diameter (including processes)  $51\text{--}77\ \mu$  (mean  $64\ \mu$ ); diameter of spore body  $26\text{--}39\ \mu$  (mean  $32\ \mu$ ).

*Remarks.* On the basis of a single specimen, Hacquebard and Barss (1957) proposed the assignment of *Zonotriletes duplicatus* (Naumova) to their new genus *Labiadensites*, which was said to differ from *Densosporites* in its invariable possession of 'a strong trilete and greatly developed lips'. It is evident from the examination of numerous Spitsbergen representatives that lips are only sporadically and never strongly developed in this species; furthermore, the earlier descriptions and illustrations given by Reinsch (1884) and Lubert and Waltz (1938) contain no reference to such laesurate modification. Hence the species seems more suitably included within *Densosporites*, as advocated by Potonié and Kremp (1956, p. 115).

*Previous records.* *Densosporites duplicatus* was first recorded by Reinsch (1884) from Russian 'Stigmarienkohle' of presumably Lower Carboniferous age. More recently, the species has been reported from Lower Carboniferous deposits of the Moscow Basin and Kizel and Selizharovo regions, U.S.S.R. (Lubert and Waltz 1938, 1941); and from Upper Mississippian coal of the South Nahanni River area, Northwest Territories, Canada (Hacquebard and Barss 1957).

### *Densosporites striatiferus* Hughes and Playford 1961

Plate 88, figs. 12, 13

*Dimensions* (40 specimens). Overall equatorial diameter  $44\text{--}65\ \mu$  (mean  $54\ \mu$ ); diameter of spore body  $27\text{--}45\ \mu$  (mean  $35\ \mu$ ); width of cingulum  $6\text{--}12\ \mu$  (mean  $9\ \mu$ ).

### *Densosporites spitsbergensis* sp. nov.

Plate 89, figs. 1–5

*Diagnosis.* Spores radial, trilete; amb subtriangular, more or less conformable with body outline. Laesurae perceptible to distinct, straight or slightly sinuous; extending on to cingulum as thickened, elevated ridges which often attain equatorial margin. Spore body convexly subtriangular, exine often poorly preserved or absent. Cingulum robust, darker in colour than body; slight and gradual equatorial decrease in thickness. Prominent spinose sculpture on distal surface of spores (body and cingulum); spines

crowded and frequently coalescent around inner margin of cingulum, reduced in size and density in equatorial region; length of spines  $1.5\text{--}5\ \mu$ , basal diameter  $1\text{--}2.5\ \mu$ . Proximal surface of spores laevigate to sparsely granulate or spinose.

*Dimensions* (100 specimens). Overall equatorial diameter  $55\text{--}80\ \mu$  (mean  $66\ \mu$ ); diameter of spore body  $23\text{--}39\ \mu$  (mean  $31\ \mu$ ).

*Holotype*. Preparation P163/3, 22.2 96.8. L.1146.

*Locus typicus*. Birger Johnsonfjellet (sample G1089), Spitsbergen; Lower Carboniferous.

*Description*. Holotype convexly subtriangular,  $64\ \mu$  overall; spore-body diameter  $28\ \mu$ ; laesurae distinct, extending to equatorial margin. The species is characterized by its conspicuous distal spinose sculpture, long laesurae, and well-developed cingulum which shows slight reduction in thickness towards the equator; it is a common microfloral constituent of many of the Spitsbergen samples.

*Comparison*. *Densosporites pannosus* Knox 1950 (p. 326; pl. 18, fig. 267) is more uniformly and comprehensively spinose and has more prominent, laesurate lips.

*Remarks*. The *spores dispersae* described above as *Densosporites spitsbergensis* sp. nov. compare closely in all respects with the microspores obtained by Bharadwaj (1959, p. 70; pl. 2, figs. 8–14) from the fructification *Porostrobis zeilleri* Nathorst 1914, which had been collected in 1882 by Nathorst from the Culm (Lower Carboniferous) at Pyramiden, Spitsbergen. Furthermore, representatives occurring in poorly preserved or overmacerated preparations are very similar to the microspores (from *P. zeilleri*) which Bharadwaj had treated with excessive potassium hydroxide. From the widespread occurrence of *D. spitsbergensis* it seems reasonable to assume concomitant widespread distribution of *P. zeilleri* in Spitsbergen during Lower Carboniferous times.

#### EXPLANATION OF PLATE 89

All figures  $\times 500$ , and from unretouched negatives.

Figs. 1–5. *Densosporites spitsbergensis* sp. nov. 1, Holotype; proximal surface. 2, Distal surface; preparation P162/5, 50.7 104.9 (L.1147). 3, Proximal surface; preparation P163/1, 27.0 96.5 (L.1148). 4, Distal surface; preparation P148/4, 44.2 107.3 (L.1149). 5, Proximal surface; preparation P164/2, 42.3 103.2 (L.1150).

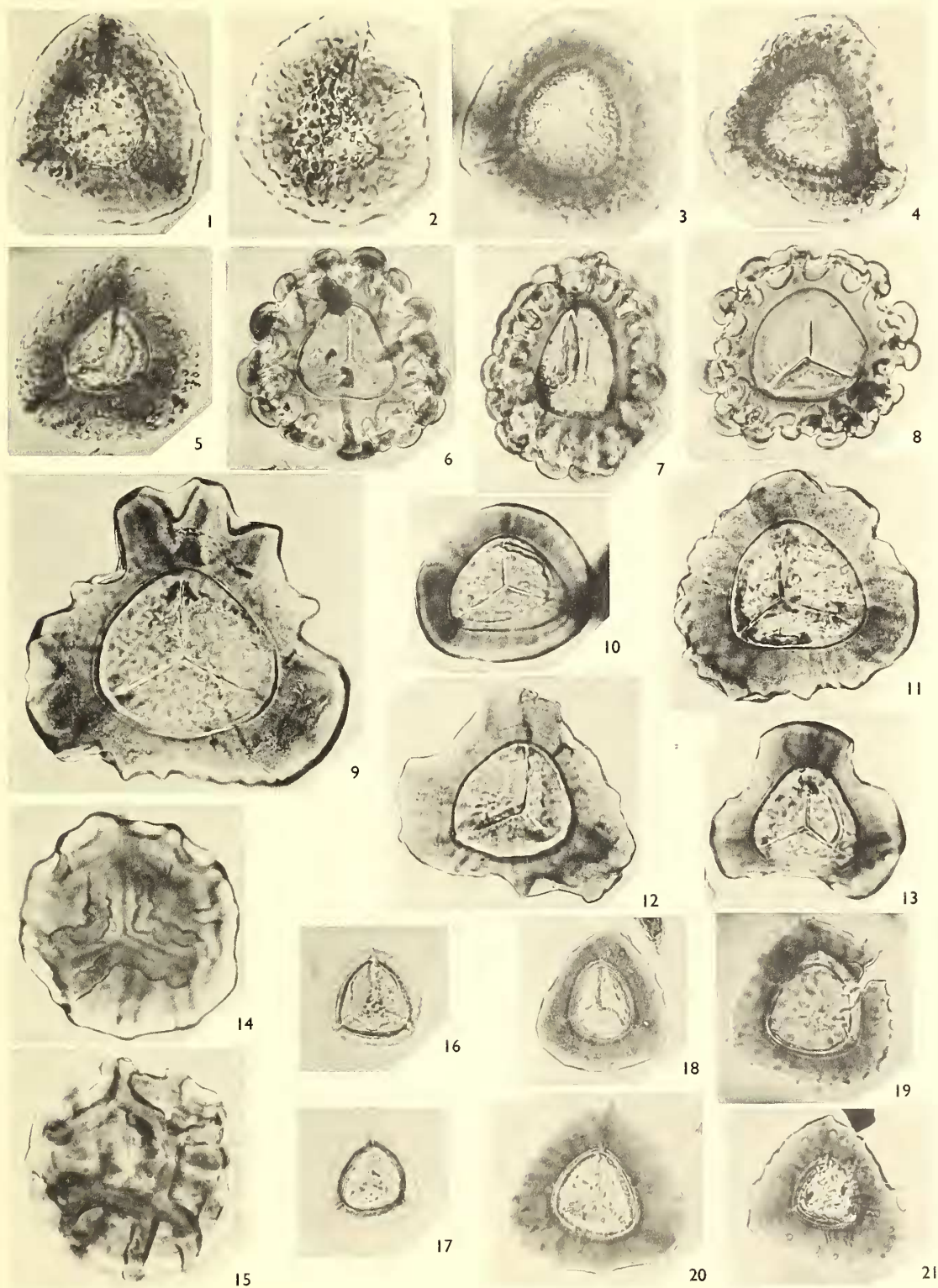
Figs. 6–8. *Densosporites duplicatus* (Naumova) Potonié and Kremp 1956. 6, Proximal surface; preparation P145A/1, 45.0 110.0 (L.1141). 7, Proximal surface; preparation P145B/1, 23.1 104.7 (L.1142). 8, Proximal surface; preparation P145B/27, 26.3 103.2 (L.1143).

Figs. 9–13. *Densosporites variomarginatus* sp. nov. 9, Proximal surface; preparation P148/56, 39.2 103.7 (L.1153). 10, Proximal surface; preparation P162/6, 30.0 106.4 (L.1154). 11, Holotype; proximal surface. 12, Proximal surface; preparation P148/27, 35.3 104.5 (L.1156). 13, Proximal surface; preparation P163/6, 38.9 101.2 (L.1155).

Figs. 14, 15. *Knoxisporites cinctus* (Waltz) Butterworth and Williams 1958. Proximal and distal surfaces respectively; preparation P163/7, 30.4 98.9 (L.1170).

Figs. 16, 17. *Lycospora uber* (Hoffmeister, Staplin, and Malloy) Staplin 1960. 16, Distal surface; preparation P180B/1, 52.8 105.0 (L.1180). 17, Proximal surface; preparation P180B/4, 43.7 106.4 (L.1181).

Figs. 18–21. *Densosporites rarispinosus* sp. nov. 18, Proximal surface; preparation P180B/1, 51.5 101.5 (L.1159). 19, Distal surface; preparation P145C/2, 34.7 107.3 (L.1160). 20, Holotype; proximal surface. 21, Distal surface; preparation P145B/1, 17.9 96.7 (L.1161).







*Densosporites variomarginatus* sp. nov.

Plate 89, figs. 9–13

*Diagnosis.* Spores radial, trilete, subtriangular. Equatorial margin irregular, i.e. smooth, undulating, dentate or lobate. Laesurae distinct, simple, usually straight, almost attaining spore-body margin. Body laevigate, sometimes finely wrinkled; outline subtriangular with rounded apices and convex to slightly concave sides. Cingulum relatively dense, laevigate or with punctations arranged parallel to spore-body outline. Cingulum may be perceptibly to distinctly radiating or striated appearance due apparently to an alternation of intrinsic, non-elevated, usually poorly defined radial 'bands' of differing thickness; the breadth of these bands is (collectively) highly variable.

*Dimensions* (100 specimens). Overall equatorial diameter 44–102  $\mu$  (mean 68  $\mu$ ); diameter of spore body 27–55  $\mu$  (mean 39  $\mu$ ); (maximum) width of cingulum 7–27  $\mu$  (mean 15  $\mu$ ).

*Holotype.* Preparation P148/62, 40·8 104·9. L.1152.

*Locus typicus.* Triungen (sample G1472), Spitsbergen; Lower Carboniferous.

*Description.* Holotype 77  $\mu$  overall; spore body microrugulate, outline convexly subtriangular, diameter 43  $\mu$ ; cingulum concentrically and finely punctate, width fairly uniform (c. 17  $\mu$ ), overall distinctly radiating appearance; equatorial margin irregularly undulating.

Despite its generally ill-defined nature (particularly in well-preserved specimens), the radially striated structure of the cingulum is always recognizable. Corrosion, either natural or in preparation, appears to have the effect of emphasizing the structure by embaying the thinner, radial areas, and resulting in an undulating or distinctly lobed equatorial margin. Thus the highly variable nature of the periphery of the cingulum, ranging as a continuous variation from entire to deeply and irregularly incised, is considered to be the result of a concomitant variation in preservation from excellent to poor, respectively. That the margin of the cingulum is highly susceptible to corrosive attack is indicated by the comparative scarcity, even in generally well-preserved assemblages, of specimens possessing an entire, uniformly broad cingulum, and further by the invariable absence of such specimens in poorly preserved assemblages. In some specimens the cingulum appears thickest about the triangular apices of the body.

*Comparison.* *Densosporites striatus* (Knox 1950, p. 330; pl. 19, fig. 289) Butterworth and Williams 1958 differs from *D. variomarginatus* sp. nov. in having a cingulum that is differentiated into an inner thickened portion and an outer, distinctly thinner zone. The cingulum of *D. subcrenatus* (Waltz) Potonié and Kremp 1956 is marginally crenulate and of essentially uniform, certainly non-striated appearance. *Tendosporites subcrenatus* (non Waltz) Hacquebard and Barss 1957 (p. 36; pl. 5, figs. 3, 4) has shorter laesurae than *D. variomarginatus* and is further distinguished by the irregular peripheral thickening of its cingulum, which is otherwise of approximately the same density as the spore body. *D. heterotomus* (Waltz in Luber and Waltz 1938, pp. 19–20; pl. 2, fig. 28) Potonié and Kremp 1956 may be similar to *D. variomarginatus*. The drawing given by Luber and Waltz depicts a striate cingulum, which is not, however, described as such in the text or evident from type 612 of Reinsch (1884, p. 60; pl. 38, fig. 257) with which Waltz equated her species. Moreover, and in contrast with *D. variomarginatus*, *D. heterotomus* possesses

thickened laesurate lips, is often granulate, and generally much larger (95–120  $\mu$ ). *D. striatiferus* Hughes and Playford 1961 has much finer and more closely spaced cingulate striations than *D. variomarginatus*.

*Densosporites rarispinosus* sp. nov.

Plate 89, figs. 18–21; text-fig. 10d

*Diagnosis.* Spores radial, trilete; amb more or less conformable with convexly sub-triangular spore-body outline. Laesurae simple, perceptible to distinct, straight or sinuous, extending equatorially 2–4  $\mu$  beyond body margin. Conspicuous distal sculpture of sparsely and irregularly distributed simple spines, which usually project also from equatorial margin; spinae variable in height (1–6  $\mu$ ), bases circular or subcircular (diameter 0.5–3  $\mu$ ); subordinate, small verrucae occasionally additionally present. Apart from this sculpture, spore body and cingulum laevigate to finely punctate (corroded specimens). Cingulum non-tapering, and much darker in colour than spore body.

*Dimensions* (60 specimens). Overall equatorial diameter 37–67  $\mu$  (mean 51  $\mu$ ); diameter of spore body 18–33  $\mu$  (mean 24  $\mu$ ).

*Holotype.* Preparation P145C/1, 49.6 98.1. L.1158.

*Locus typicus.* Triungen (sample G1466), Spitsbergen; Lower Carboniferous.

*Description.* Holotype 53  $\mu$  overall, spore body 27  $\mu$ ; irregularly disposed distal spinae 1.5–6  $\mu$  long, 1–2.5  $\mu$  broad at base, 4–12  $\mu$  apart, progressively sparser towards equator; cingulum and body otherwise infrapunctate; sinuous laesurae extending on to cingulum, 2  $\mu$  beyond body margin. This distinctive species is characterized by sparse, but conspicuous, spinose distal sculpture, together with consistent slight extension of the laesurae into the cingulum.

*Remarks.* Smith (1960) has demonstrated the existence of two distinct wall layers in several species of *Densosporites* and *Anulatisporites*—namely an inner membrane (intexine) forming the ‘central body’ and an outer layer (exoexine) which is equatorially expanded and thickened, thus constituting the cingulum. A similar wall construction is evident in *Densosporites rarispinosus* sp. nov.; probably overmacerated specimens (e.g. Pl. 89, fig. 19) show a more or less distinct separation of the two wall layers. The same effect has been discussed and illustrated by Bharadwaj (1959, p. 70; pl. 2, figs. 13, 14) in the case of excessively macerated, *Densosporites*-type microspores of the fructification *Porostrobis zeillerei* Nathorst.

*Comparison.* *Densosporites spinifer* Hoffmeister, Staplin, and Malloy 1955b (pp. 386–7; pl. 36, figs. 16, 17) differs from *D. rarispinosus* in possessing a coarsely granulate, relatively larger, non-spinose spore body; the spinae of *D. spinifer* are often closely packed and apparently developed on both proximal and distal surfaces of the cingulum. *D. brevispinosus* Hoffmeister, Staplin, and Malloy 1955b (p. 386; pl. 36, fig. 22) is sub-circular and has a variably differentiated, minutely spinose cingulum enclosing a granulate spore body. The spinose sculpture of *D. spinosus* Dybová and Jachowicz 1957 (pp. 164–5; pl. 49, figs. 1–4) is more strongly developed than in *D. rarispinosus*, the cingulum thickness decreases equatorially and the proximal surface is granulate. *D.*



*dentatus* (Waltz) Potonié and Kremp 1956 has a regularly dentate equatorial margin, but is laevigate or granulate on the proximal and distal surfaces.

*Densosporites aculeatus* sp. nov.

Plate 88, figs. 16, 17; text-fig. 10e

*Diagnosis.* Spores radial, trilete; amb conformable with convexly subtriangular outline of spore body. Laesurae indistinct, simple, straight to curved or sinuous, extending to, or just beyond, body margin; frequently not preserved owing to fragility of proximal body wall. Width and thickness of cingulum fairly uniform, colour much darker than spore body. Equatorial margin and whole of distal surface bear numerous, stout, conspicuously tapering, simple spinae, which have  $\pm$  circular bases and are variably spaced (but rarely coalescent); length of spines  $2.5\text{--}9\ \mu$  (usually about  $5\ \mu$ ), basal diameter  $1.5\text{--}5\ \mu$  (average  $3.5\ \mu$ ). Apart from spinose sculpture—spore body laevigate to infra-granulate, cingulum laevigate (irregularly punctate in corroded specimens).

*Dimensions* (36 specimens). Overall equatorial diameter (excluding spinose projections)  $31\text{--}57\ \mu$  (mean  $43\ \mu$ ); diameter of spore body  $18\text{--}32\ \mu$  (mean  $26\ \mu$ ).

*Holotype.* Preparation P164/3, 22.3 96.9. L.1163.

*Locus typicus.* Birger Johnsonfjellet (sample G1095), Spitsbergen; Lower Carboniferous.

*Description.* Holotype roundly subtriangular,  $40\ \mu$  overall; prominently spinose distally and (particularly) equatorially; spinae  $4\text{--}7\ \mu$  long,  $3\text{--}4\ \mu$  broad at base; cingulum otherwise laevigate, spore body finely granulate; body diameter  $28\ \mu$ .

*Comparison.* *Densosporites aculeatus* sp. nov. resembles *D. spinifer* Hoffmeister, Staplin, and Malloy 1955b (pp. 386–7; pl. 36, figs. 16, 17), but differs in bearing spines on the distal surface of the spore body. *Spinozonotriletes*? *exiguus* Staplin 1960 (p. 22; pl. 4, figs. 26–28) is circular and has comparatively short laesurae, but otherwise seems very similar to *D. aculeatus*. Another closely allied species is *D. rarispinosus* sp. nov.; this is distinguishable, however, in its much less strongly developed spinose sculpture, and always clearly discernible laesurae.

*Densosporites* sp.

Plate 88, fig. 18

*Description of specimens.* Spores radial, trilete; amb roundly subtriangular. Laesurae distinct, simple, straight, extending to spore-body margin. Body subtriangular with straight to slightly convex sides and rounded to somewhat pointed apices; laevigate or faintly punctate, irregularly thickened on distal surface. Broad cingulum of fairly uniform width and similar density to spore body; sculpture irregularly and minutely scabrate to areolate, particularly in equatorial region.

*Dimensions* (2 specimens). Overall equatorial diameter  $77\text{--}92\ \mu$ ; diameter of spore body  $37\text{--}40\ \mu$ .

*Comparison.* The only comparable species to have appeared in the literature is *Zonotriletes latizonalis* Waltz (in Luber and Waltz 1941, p. 32; pl. 6, fig. 92); this differs from the specimens described above in its marginally serrate cingulum and smaller spore body (diameter  $20\text{--}25\ \mu$ ).

## Genus LABIADENSITES Hacquebard and Barss 1957

*Type species.* *L. attenuatus* Hacquebard and Barss 1957.

*Affinity.* Unknown.

*Labiadensites fimbriatus* (Waltz) Hacquebard and Barss 1957

Plate 90, figs. 1–3

1938 *Zonotriteles fimbriatus* Waltz in Luber and Waltz, p. 20; pl. 2, fig. 25.

1956 *Hymenozonotriteles fimbriatus* (Waltz) Ishchenko, p. 63; pl. 12, fig. 133.

1956 *Densosporites fimbriatus* (Waltz) Potonié and Kremp, p. 115.

1957 *Labiadensites fimbriatus* (Waltz) Hacquebard and Barss, p. 28; pl. 4, fig. 2.

*Description of specimens.* Spores radial, trilete; amb circular to subcircular. Laesurae distinct, straight, almost attaining spore-body margin; flanked by broad, flat lips extending 6–10  $\mu$  on either side of laesurae and having undulating outer margins. Spore body laevigate to infrapunctate. Cingulum smooth, dense; encompassed by a more translucent, less robust equatorial border, which has a frilled, rather membranous appearance; boundary between these is usually well defined and conformable with the smooth, circular spore-body margin. Some specimens were observed in which the membranous border overlaps rather irregularly on to the inner part of the cingulum, particularly on its distal surface. Also, the outer portion sometimes shows considerable variation in width on any one specimen (see Pl. 90, fig. 1), in which case the equatorial outline is broadly undulating.

*Dimensions* (75 specimens). Overall equatorial diameter 90–144  $\mu$  (mean 115  $\mu$ ); diameter of spore body 50–88  $\mu$  (mean 69  $\mu$ ).

*Comparison.* *Zonotriteles ciliato-marginatus* Waltz (in Luber and Waltz 1941, pp. 21–22; pl. 4, fig. 52) has similar, but less concise, differentiation of the cingulum, the outer portion of which is thickly covered with small projections. Some specimens of *L. fimbriatus* (e.g. Pl. 90, fig. 3), in which the outer membranous border has been partially removed, appear as transitional forms linking this species with *Anulatisporites labiatus* Hughes and Playford 1961, which has a smooth undifferentiated cingulum. Thus the two species may well be closely related.

## EXPLANATION OF PLATE 90

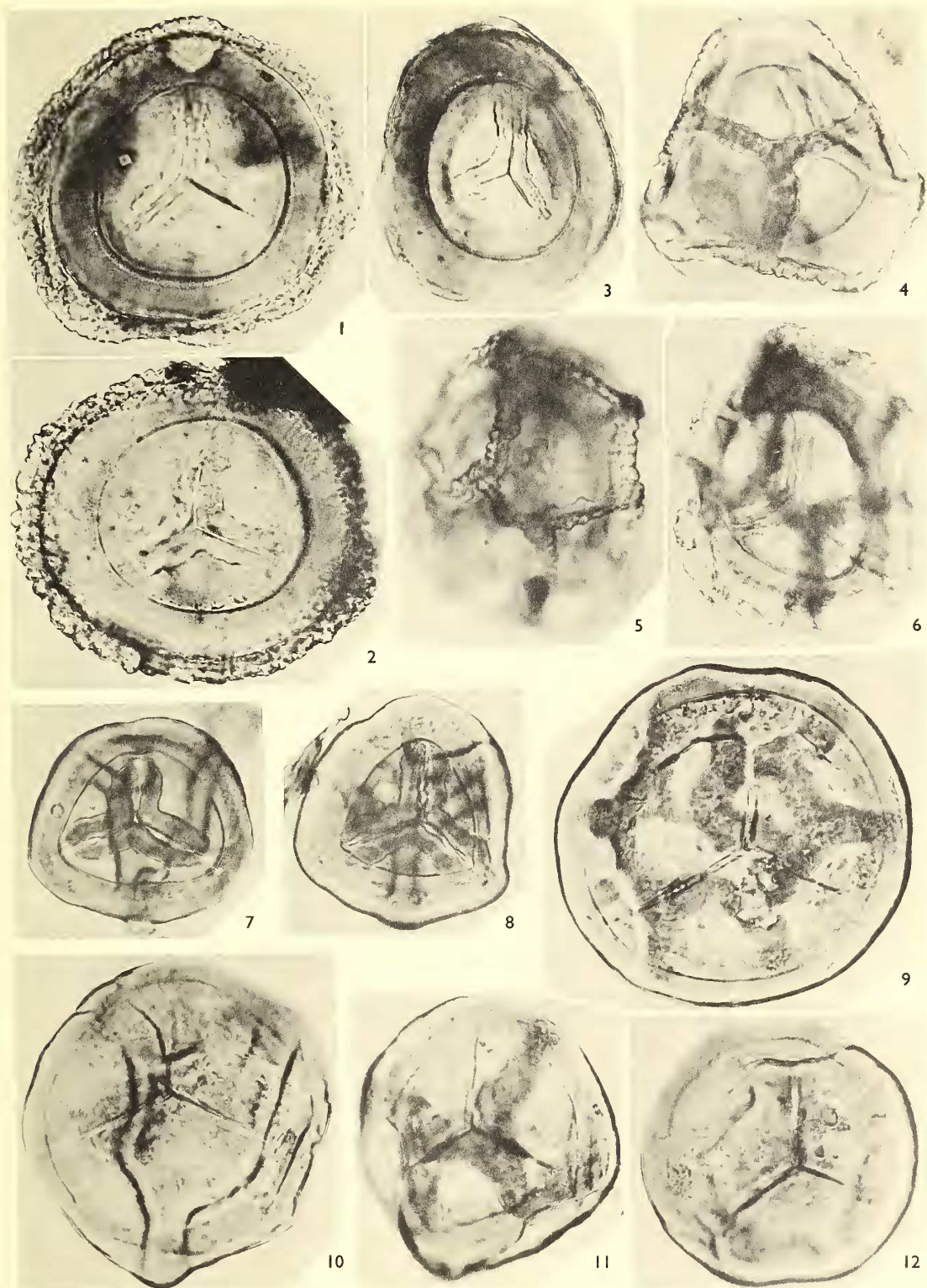
All figures  $\times 500$ , and from unretouched negatives.

Figs. 1–3. *Labiadensites fimbriatus* (Waltz) Hacquebard and Barss 1957. 1, Distal surface; preparation P148/41, 34.0 106.6 (L.1167). 2, Proximal surface; preparation P148/5, 52.4 108.9 (L.1168). 3, Proximal surface; preparation P163/7, 27.1 111.3 (L.1169).

Figs. 4–6. *Knoxisporites margarethae* Hughes and Playford 1961. 4, Distal surface; preparation P173/1, 20.2 112.5 (L.1171). 5, 6, Distal and proximal surfaces respectively; preparation M811/1, 42.5 110.4 (L.1172).

Figs. 7, 8. *Knoxisporites literatus* (Waltz) comb. nov. 7, Proximal surface; preparation P163/7, 47.7 107.2 (L.1173). 8, Proximal surface; preparation P163/7, 31.4 102.8 (L.1174).

Figs. 9–12. *Knoxisporites hederatus* (Ishchenko) comb. nov. 9, Proximal surface; preparation P181/5, 35.3 95.8 (L.1178). 10, Proximal surface; preparation P148/5, 47.7 112.8 (L.1175). 11, Proximal surface; preparation P148/5, 24.4 100.9 (L.1177). 12, Proximal surface; preparation P148/55, 37.8 105.4 (L.1176).



PLAYFORD, Lower Carboniferous microspores





*Previous records.* This distinctive species was apparently widespread in the Northern Hemisphere during Lower Carboniferous times, with previous records from the Tournaisian–Viséan of the Moscow Basin and Kizel region (Luber and Waltz 1938, 1941); from the Tournaisian of the western Donetz Basin (Ishchenko 1956); from the Viséan of the Dnieper–Donetz Basin (Ishchenko 1958); and from Upper Mississippian coal of the South Nahanni River area, Northwest Territories, Canada (Hacquebard and Barss 1957).

Genus *KNOXISPORITES* (Potonié and Kremp) Neves 1961

*Type species.* *K. hageni* Potonié and Kremp 1954.

*Discussion.* Neves (1961) has emended the diagnosis of *Knoxisporites* Potonié and Kremp 1954, and thereby transferred the genus from the Murornati to the Cingulati. Certainly many of the species (including the type) assigned to *Knoxisporites* appear to be definitely cingulate, in addition to their possession of prominent muri variously arranged on the distal hemisphere. In many instances, however, the distinction between cingulum and equatorially disposed mura would not seem as clear as is implied by Neves (1961).

*Knoxisporites* may be considered analogous to *Lophozonotriletes* (Naumova) Potonié 1958, differing mainly in sculptural characteristics.

*Affinity.* Unknown.

*Knoxisporites cinctus* (Waltz) Butterworth and Williams 1958

Plate 89, figs. 14, 15

1938 *Zonotriletes cinctus* Waltz in Luber and Waltz, p. 22 (no description); pl. 2, fig. 27.

1956 *Annlatisporites cinctus* (Waltz) Potonié and Kremp, p. 111.

1958 *Euryzonotriletes cinctus* (Waltz) Ishchenko, table 3.

1958 *Knoxisporites cinctus* (Waltz) Butterworth and Williams, p. 370; pl. 2, figs. 11–13.

*Dimensions* (45 specimens). Overall equatorial diameter 58–94  $\mu$  (mean 75  $\mu$ ); diameter of spore body 38–69  $\mu$  (mean 54  $\mu$ ).

*Previous records.* *Knoxisporites cinctus* (Waltz) has been reported previously (a) from Russia by Luber and Waltz (1938, 1941) from the Lower Carboniferous of the Voronezh and Selizharovo districts, and by Ishchenko (1958) from Namurian rocks of the Dnieper–Donetz Basin; (b) from Scotland by Butterworth and Williams (1958) from the upper part of the Limestone Coal Group (Namurian A); (c) from one sample (B685) of the Lower Carboniferous of Spitsbergen (Hughes and Playford 1961).

*Knoxisporites margarethae* Hughes and Playford 1961

Plate 90, figs. 4–6

*Remarks.* Study of numerous additional specimens has indicated that the species is definitely cingulate, with the distal thickened ring developed at or near the cingulum/spore-body margin; and further that the distal extra-reticulum appears to be supported by, although distinct from, the smooth distal muri.

*Dimensions* (70 specimens). Overall equatorial diameter 64–117  $\mu$  (mean 90  $\mu$ ); diameter of spore body 37–74  $\mu$  (mean 53  $\mu$ ).

*Knoxisporites literatus* (Waltz) comb. nov.

Plate 90, figs. 7, 8

1938 *Zonotriletes literatus* Waltz in Luber and Waltz, p. 18; pl. 2, fig. 21, and pl. A, fig. 11.1956 *Euryzonotriletes literatus* (Waltz) Ishchenko, pp. 52–53; pl. 9, fig. 108.1956 *Anulatisporites literatus* (Waltz) Potonié and Kremp, p. 111.1957 *Cincturasporites literatus* (Waltz) Hacquebard and Barss, pp. 23–24; pl. 3, figs. 2–5.

*Description of specimens.* Spores radial, trilete; amb convexly subtriangular, smooth or may show gentle undulation. Laesurae distinct, straight, length equal to, or slightly less than, spore-body radius; bordered by broad, smooth, flat lips which extend approximately 6–10  $\mu$  on either side of laesurae. Cingulum broad, usually regular, width 8–19  $\mu$ ; inner margin sometimes darker in colour, possibly indicating poleward extension (3–5  $\mu$ ) over spore body. In some specimens the cingulum is slightly narrower at the apices, so that the amb tends to appear more roundly triangular than the equatorial outline of the spore body. Distal surface has characteristic sculpture of several (usually three or four) smooth, rounded muri, which are rather irregularly disposed and often loosely connected; width of muri 6.5–12  $\mu$ . Apart from lips and distal muri, spore body and cingulum laevigate.

*Dimensions* (75 specimens). Overall equatorial diameter 56–102  $\mu$  (mean 76  $\mu$ ); diameter of spore body 42–74  $\mu$  (mean 56  $\mu$ ). This corresponds closely to the combination of the dimensions reported for the species by Waltz (in Luber and Waltz 1938), Ishchenko (1956, 1958), and Hacquebard and Barss (1957).

*Remarks.* This cingulate species, possessing well-developed distal muri, is conformable with *Knoxisporites* Potonié and Kremp as emended by Neves (1961). The ‘overlap’ of the cingulum on to the spore body is infrequently apparent and it was not mentioned in the original specific diagnosis (Waltz in Luber and Waltz 1938, p. 18); thus assignment to *Cincturasporites* Hacquebard and Barss 1957 is unacceptable.

*Previous records.* This characteristically Lower Carboniferous species has been reported previously from the U.S.S.R. (Luber and Waltz 1938, 1941; Ishchenko 1956, 1958), Canada (Hacquebard and Barss 1957), and Spitsbergen (Hughes and Playford 1961). Probable representatives occur also in the Upper Devonian of Western Australia (Balme and Hassell 1962, p. 11). On the basis of vertical distribution studies in the Dnieper–Donetz Basin, Ishchenko (1958, stratigraphical range table 3) indicates a range from Upper Devonian to Namurian.

*Knoxisporites hederatus* (Ishchenko) comb. nov.

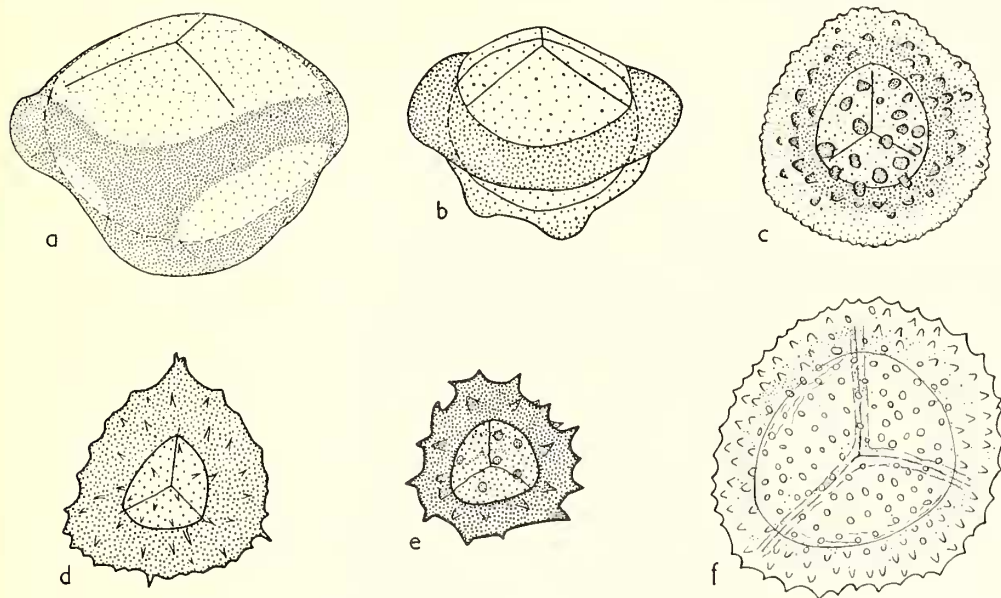
Plate 90, figs. 9–12; text-fig. 10a

1956 *Euryzonotriletes hederatus* Ishchenko, pp. 58–59; pl. 10, fig. 121.

*Description of specimens.* Spores radial, trilete; amb circular to subcircular. Distinct spore body encompassed by more or less conformable cingulum (width 6–16  $\mu$ , mean 11  $\mu$ ). Laesurae distinct, simple, straight, length three-quarters of, to almost equal to, spore-body radius. Distal hemisphere bears conspicuous, widely spaced, relatively low, broad, smooth, rounded muri, which are connected in several places to each other and to the cingulum, but do not form a constant, symmetrical pattern; muri slightly sinuous,

breadth 8–17  $\mu$ , height 4–7  $\mu$ . Apart from muri, exine laevigate to infrapunctate (oil immersion). Marginal distortion, particularly of muri, common.

*Dimensions* (40 specimens). Overall equatorial diameter 67–112  $\mu$  (mean 86  $\mu$ ). Thus the Spitsbergen representatives suggest a considerably less restricted size range for the species than that stated by Ishchenko (1956, 1958) as 85–90  $\mu$ .



TEXT-FIG. 10. Camera lucida drawings; all magnifications  $\times 500$  unless otherwise specified. *a*, *Knoxisporites hederatus* (Ishchenko) comb. nov.; lateral view; preparation P174/2, 41.2 114.2 (L.1179). *b*, *Lophozonotriteles appendices* (Hacquebard and Barss) comb. nov. ( $\times 250$ ); lateral view; preparation P154/5, 53.2 108.7 (L.1190). *c*, *L. variverrucatus* sp. nov.; distal surface; preparation P175/2, 33.9 109.0 (L.1193). *d*, *Densosporites rarispinosus* sp. nov.; distal surface; preparation P145A/1, 25.6 98.0 (L.1162). *e*, *D. aculeatus* sp. nov.; distal surface; preparation P164/2, 43.5 93.3 (L.1165). *f*, *Cristatisporites echinatus* sp. nov.; distal surface; preparation P148/1, 31.9 108.9 (L.1184).

*Remarks.* This species is included within *Knoxisporites* on the basis of its conspicuous distal sculpture of strongly developed muri together with distinct equatorial girdle. The subgroup *Euryzonotriteles* Naumova 1939 is an unsatisfactory taxon as it embraces many valid genera, and, as noted by Potonié (1956, p. 87), it appears to lack a type species.

*Previous records.* According to Ishchenko (1956, 1958) this species is confined to sediments of Tournaisian–Lower Viséan age in the western extension of the Donetz Basin; and to Tournaisian–Viséan strata in the Dnieper–Donetz Basin.

#### Genus LYCOSPORA (Schopf, Wilson, and Bentall) Potonié and Kremp 1954

*Type species.* *L. micropapillata* (Wilson and Coe) Schopf, Wilson, and Bentall 1944.

*Affinity.* Schopf, Wilson, and Bentall (1944, p. 54) considered that most of the isolated spores conformable with their genus *Lycospora* represent microspores of arborescent



lepidodendrids. Subsequently, Potonié and Kremp (1954, p. 156) allied the genus with the Lepidophytales, Lepidodendraceae, and Lepidospermales.

Chaloner (1953b) obtained microspores conformable with *Lycospora* from two heterosporous lycopod strobili, *Lepidostrobus dubius* Binney and *L. russelianus* Binney, both of Upper Carboniferous age. In 1958 Sen reported microspores similar to *Lycospora parva* Kosanke 1950 from *Lepidostrobus goldenbergi* Schimper and from *L. variabilis* Lindley and Hutton.

*Lycospora uber* (Hoffmeister, Staplin, and Malloy) Staplin 1960

Plate 89, figs. 16, 17

- 1938 *Zonotriletes pusillus* (non Ibrahim) Waltz in Luber and Waltz, p. 15; pl. 3, fig. 33, and pl. A, fig. 12.
- 1941 *Zonotriletes pusillus* (non Ibrahim) var. *gracilis* Waltz in Luber and Waltz, p. 35; pl. 7, fig. 101b.
- 1952 *Hymenozonotriletes pusillus* (non Ibrahim) Ishchenko, p. 50; pl. 13, fig. 122.
- 1955 *Cirratiradites uber* Hoffmeister, Staplin, and Malloy, p. 383; pl. 36, fig. 24.
- 1957 *Hymenozonotriletes pusillus* (non Ibrahim) Naumova; Byvsheva, p. 1010.
- 1960 *Lycospora uber* (Hoffmeister, Staplin, and Malloy) Staplin, p. 20; pl. 4, figs. 13, 17, 18, 20.

*Description of specimens.* Spores radial, trilete; amb convexly subtriangular, conformable with spore-body outline. Laesurae distinct, straight, length approximately equal to body radius; accompanied by narrow, more or less prominent lips. Spore body subtriangular with convex sides and rounded apices; finely granulate to finely rugulate/verrucate (distal sculpture often coarser); sometimes arcuately folded at periphery. Cingulum ('flange') narrow, laevigate, often diaphanous; equatorial margin smooth in well-preserved specimens.

*Dimensions* (50 specimens). Overall equatorial diameter 26–39  $\mu$  (mean 32  $\mu$ ); diameter of spore body 19–27  $\mu$  (mean 23  $\mu$ ).

*Remarks.* The numerous species listed by Staplin (1960, p. 20) as synonymous with *Lycospora uber* (Hoffmeister, Staplin, and Malloy) is a reflection of the variable nature of this species, which is often extremely abundant in the Spitsbergen samples. *L. uber* is undoubtedly conspecific with forms incorrectly assigned by Russian authors (Waltz, Ishchenko, Byvsheva, &c.) to Ibrahim's species, i.e. *L. pusilla* (Ibrahim) Schopf, Wilson, and Bentall. Staplin also lists a number of other species, such as *L. noctuina* Butterworth and Williams 1958 (p. 376; pl. 3, figs. 14, 15), which may well also be representative of *L. uber*. Certainly much specific subdivision of spores in this category has resulted from their susceptibility to corrosion, and consequent somewhat variable appearance, particularly with respect to spore-body sculpture. As noted by Staplin (1960), a detailed reappraisal of the types of all species included within *Lycospora* would seem an essential approach to the problem.

*Previous records.* This species has been recorded by numerous authors from the Russian Carboniferous (Luber and Waltz 1938, 1941; Ishchenko 1952, 1956, 1958; Byvsheva 1957, &c.) and also from the Upper Mississippian of North America (Hoffmeister, Staplin, and Malloy 1955; Hacquebard and Barss 1957; Staplin 1960). Future proven synonymy may show its presence in the Namurian assemblages described by Dybová and Jachowicz (1957) and Butterworth and Williams (1958). As indicated by Ishchenko



(1958, stratigraphical range table 3), it seems likely that *Lycospora uber* did not appear until early Viséan times; its upper limit of distribution is, however, dependent upon resolution of the taxonomic problems discussed above.

### Genus CRISTATISPORITES Potonié and Kremp 1954

*Type species.* *C. indignabundus* (Loose) Potonié and Kremp 1954.

*Discussion.* After critical re-examination of the diplotype, and study of other Upper Carboniferous species of *Cristatisporites*, Bhardwaj (1957, p. 105) came to the conclusion that 'the spores are cingulate having a narrow, subequatorial, thickened peripheral region comparable in structure and organisation to the *cingulum* of *Densosporites* and *Lycospora*'. Richardson (1960, p. 58) followed Bhardwaj in including *Cristatisporites* within the Cingulati, an assignment which is also supported by the Spitsbergen specimens described below.

*Affinity.* Unknown.

#### *Cristatisporites echinatus* sp. nov.

Plate 91, figs. 1-4; text-fig. 10f

*Diagnosis.* Spores radial, trilete; amb convexly subtriangular. Differentiation into central area and cingulum distinct to obscure; cingulum width approximately 15-25 per cent. of amb diameter. Laesurae prominent, elevated, with thickened lips (individually 2-4.5  $\mu$  wide, and up to 4  $\mu$  high); extending on to cingulum, often attaining equatorial margin. Conspicuous echinate sculpture restricted to distal hemisphere and equator, comprising small, fairly closely spaced cones or spines, more or less uniformly distributed, and producing serrate equatorial margin. Sculptural elements  $\pm$  equal in size on any one specimen, bases circular to oval, apices pointed or slightly rounded, usually discrete, occasionally fused in small groups; basal diameter of cones/spines 1.5-4  $\mu$ , length 1.5-5  $\mu$ . Proximal hemisphere finely granulate to infrapunctate.

*Dimensions* (25 specimens). Overall equatorial diameter 63-100  $\mu$  (mean 81  $\mu$ ).

*Holotype.* Preparation P148/31, 39.7 104.2. L.1182.

*Locus typicus.* Triungen (sample G1472), Spitsbergen; Lower Carboniferous.

*Description.* Holotype 92  $\mu$  overall, width of cingulum 14-21  $\mu$ ; pronounced laesurae (lips 4  $\mu$  wide) attaining serrate equatorial margin; proximal hemisphere sparsely and unevenly granulate (grana up to 1  $\mu$  in diameter). In some specimens the distal sculpture shows a gradual, almost imperceptible increase in density towards the equator, so that the cones/spines are fairly closely packed equatorially, and comparatively sparsely distributed in the vicinity of the distal pole. Fusion of these sculptural elements, when encountered, is restricted to the equatorial region, with groups of no more than three. The cingulum usually shows some equatorial decrease in thickness which may be gradual or abrupt; in the latter instance (as with the holotype) a dark ring is evident defining the inner margin of the cingulum. The conspicuous triradiate marks usually appear as uniform, slightly roughened, relatively thick ridges in which dehiscence fissures are frequently not visible.

*Comparison.* One of two illustrations given by Lubert (1955, pl. 5, fig. 111) of *Lepidozonotriletes ciliaris* (Lubert) resembles *Cristatisporites echinatus* sp. nov., but close similarities are not apparent from either the description (p. 46) or the accompanying figure (pl. 5, fig. 112). *Hymenozonotriletes praetervisus* Naumova 1953 (pl. 4, fig. 8) may be similar, but an accurate comparison is not possible from Naumova's illustration and brief description. The subgroup *Hymenozonotriletes* Naumova appears to embrace indiscriminately monosaccate, cingulate, and zonate forms.

### Genus LOPHOZONOTRILETES (Naumova) Potonié 1958

*Type species.* *L. lebedianensis* Naumova 1953.

*Affinity.* Unknown.

### *Lophozonotriletes rarituberculatus* (Lubert) Kedo 1957

Plate 91, figs. 8, 9; text-fig. 9b

1941 *Zonotriletes rarituberculatus* Lubert in Lubert and Waltz, pp. 10, 30; pl. 1, fig. 5, and pl. 5, fig. 76.

1956 *Euryzonotriletes rarituberculatus* (Lubert) Ishchenko var. *triangulatus* Ishchenko, p. 51; pl. 8, fig. 104.

1957 *Lophozonotriletes rarituberculatus* (Lubert) Kedo, p. 1166.

1961 *Lophozonotriletes triangulatus* Hughes and Playford, pp. 35–36; pl. 3, figs. 3–7.

*Remarks.* In 1956 Ishchenko instituted the infraspecific taxon '*Euryzonotriletes rarituberculatus* (Lubert) comb. nov. var. *triangulatus* var. nov.' Specimens identical to those described by Ishchenko were recorded subsequently from Spitsbergen by Hughes and Playford (1961), who elevated the variety to specific status 'as it occurs alone in considerable numbers in sample B685'. Additional study by the present writer indicates the widespread lateral, and restricted vertical, distribution of this form within Vest-spitsbergen.

After the submission (in April 1960) of the Hughes and Playford manuscript, how-

### EXPLANATION OF PLATE 91

All figures  $\times 500$ , and from unretouched negatives.

Figs. 1–4. *Cristatisporites echinatus* sp. nov. 1–3, Holotype. Proximal view: 1, high focus; 2, central focus; 3, low focus. 4, Distal surface; preparation P175/1, 28.5 113.0 (L.1183).

Fig. 5. *Lophozonotriletes dentatus* Hughes and Playford 1961. Proximal surface; preparation P226/5, 43.3 113.1 (L.1187).

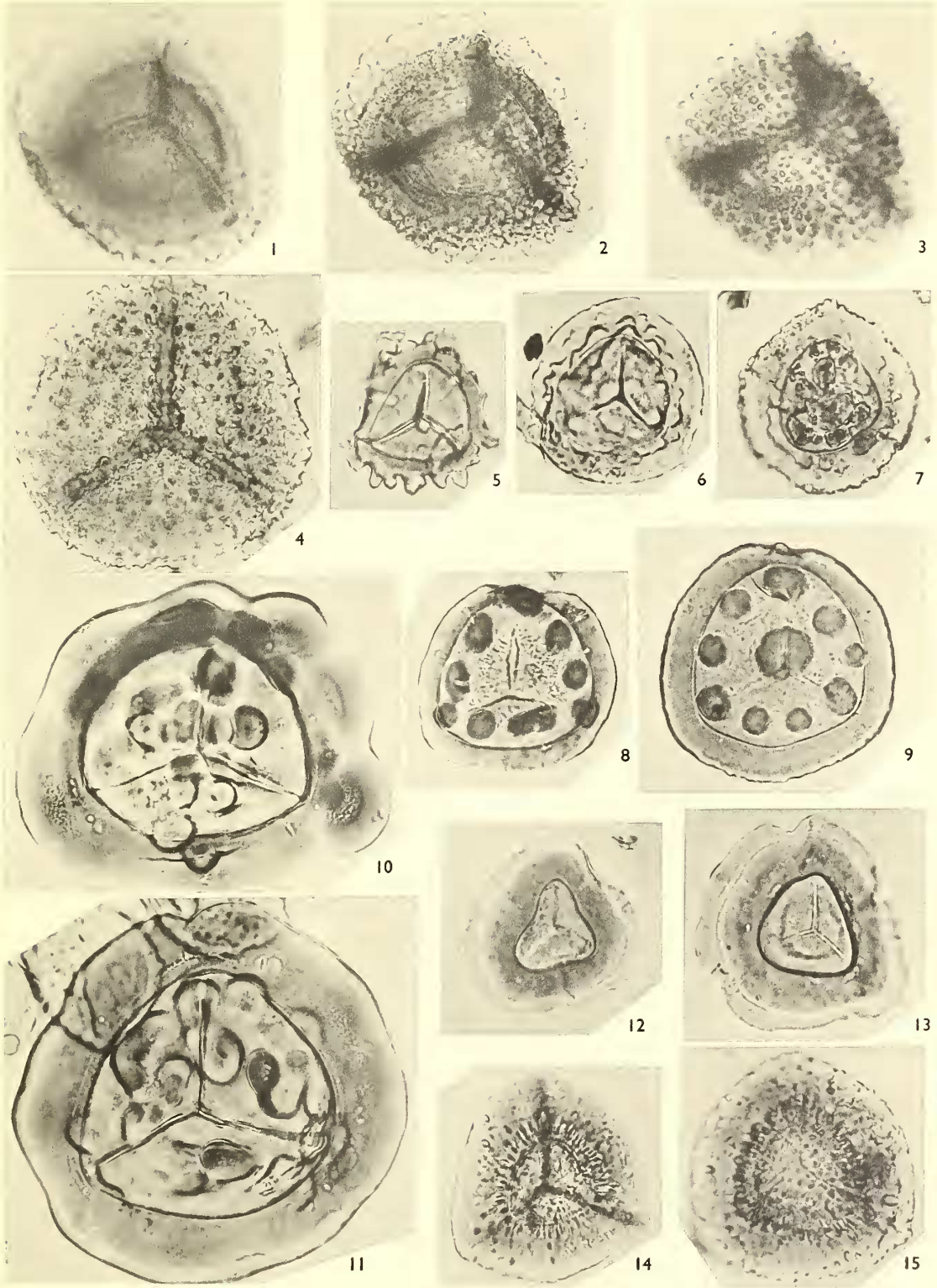
Figs. 6, 7. *Lophozonotriletes variverrucatus* sp. nov. 6, Holotype; proximal surface. 7, Distal surface; preparation M811/1, 40.5 99.6 (L.1192).

Figs. 8, 9. *Lophozonotriletes rarituberculatus* (Lubert) Kedo 1957. 8, Proximal surface; preparation P163/7, 26.2 94.6 (L.1186). 9, Distal surface; preparation P173/10, 30.3 104.2 (L.1185).

Figs. 10, 11. *Lophozonotriletes appendices* (Hacquebard and Barss) comb. nov. 10, Distal surface; preparation P149A/8, 36.3 104.7 (L.1189). 11, Proximal surface; preparation P149A/1, 17.8 113.9 (L.1188).

Figs. 12, 13. *Potoniesporites delicatus* sp. nov. 12, Holotype; proximal surface. 13, Proximal surface; preparation P149A/29, 34.0 106.4 (L. 1203).

Figs. 14, 15. *Tholisporites foveolatus* Hughes and Playford 1961. 14, Proximal surface; preparation P148/40, 36.9 104.0 (L.1200). 15, Distal surface; preparation P172/1, 30.0 104.8 (L. 1201).



PLAYFORD, Lower Carboniferous microspores





ever, the important publication of Luber and Waltz (1941) came to hand, and a detailed comparison of the diagnoses given by Luber (1941, p. 10) for the species, and by Ishchenko (1955, p. 51) for the variety, casts considerable doubt upon the validity of the latter as a distinct morphographical unit. Ishchenko considered his variety distinguishable on the basis of its 'uniformly broad border and regular roundly triangular shape'. However, Luber had clearly described *Zonotriletes rarituberculatus* as being 'roundly triangular', and although noting the margin as somewhat irregular and scallop-like, one of her illustrations (pl. 5, fig. 76: redrawn herein as text-fig. 9b) shows a more or less uniform, entire equatorial margin. It is important to note that Ishchenko included *Z. rarituberculatus* Luber in its entirety within the variety, which must itself, on this basis alone, be considered an unwarranted, superfluous institution.

Of the other illustration given by Luber (1941, pl. 1, fig. 5), which shows an undulating equatorial margin, numerous parallels exist in the Spitsbergen material; these are usually accountable as the result of either folding or corrosion.

Kedo (1957, p. 1166) included *Zonotriletes rarituberculatus* Luber, one of a number of species she listed as characteristic of the Lower Tournaisian of White Russia, within the category of *Lophozonotriletes* Naumova. This assignment remains acceptable under the emendation (by Potonié 1958, pp. 27–28) of Naumova's subgroup (cf. Hughes and Playford 1961, p. 35). *L. rarituberculatus* (Luber) is a highly distinctive species and is undoubtedly of considerable stratigraphical value (see previous records below).

*Dimensions* (100 specimens). Overall equatorial diameter 50–82  $\mu$  (mean 66  $\mu$ ); diameter of spore body 34–59  $\mu$  (mean 47  $\mu$ ); width of cingulum 5–15  $\mu$  (mean 10  $\mu$ ).

*Previous records.* Initially described (Luber in Luber and Waltz 1941) from Upper Devonian of the Timan Peninsula and Kizel region and from the lower horizons of the Tournaisian in the southern Moscow Basin and Voronezh region. Ishchenko (1956) found *L. rarituberculatus* to be restricted to Tournaisian strata of the western extension of the Donetz Basin, and Kedo (1957, 1958, 1959) to the Malevka horizon (Lower Tournaisian) of White Russia. Byvsheva (1957, 1960) reported its presence in lowermost Carboniferous from the Melekess and Busuluk deep wells and from the Volga–Ural region. Recently Hughes and Playford (1961) described the species from one sample (B685) of the Spitsbergen Lower Carboniferous, the first-reported occurrence outside the U.S.S.R.

*Lophozonotriletes dentatus* Hughes and Playford 1961

Plate 91, fig. 5

*Dimensions* (30 specimens). Overall equatorial diameter 42–69  $\mu$  (mean 55  $\mu$ ); diameter of spore body 28–48  $\mu$  (mean 37  $\mu$ ).

*Lophozonotriletes appendices* (Hacquebard and Barss) comb. nov.

Plate 91, figs. 10, 11; text-fig. 10b

1957 *Cincturasporites appendices* Hacquebard and Barss, p. 25; pl. 3, figs. 10–12.

*Description of specimens.* Spores radial, trilete; amb roundly subtriangular. Laesurae distinct, simple, straight, length approximately equal to spore-body radius. Body subtriangular with convex sides and rounded apices. Cingulum uniform or somewhat

variable in width (average  $20\ \mu$ ), laevigate to finely punctate, often exhibiting narrow concentric furrows; inner margin sometimes darker and well defined, probably indicating poleward 'overlap' ( $3\text{--}5\ \mu$ ) on spore body. Prominent distal sculpture consisting of from four to twenty-two large, smooth, rounded projections (verrucae) disposed rather irregularly on spore body and sometimes additionally on inner margin of cingulum; occasional sparse development on infrapunctate proximal surface of spore body. Verrucae subcircular to oval in surface view, basal diameter  $8\text{--}27\ \mu$ , height  $6\text{--}10\ \mu$ ; rarely coalescent, most strongly developed around distal pole. Equatorial margin smooth to undulating.

*Dimensions* (44 specimens). Overall equatorial diameter  $110\text{--}170\ \mu$  (mean  $137\ \mu$ ); diameter of spore body  $69\text{--}117\ \mu$  (mean  $90\ \mu$ ).

*Remarks.* Although generally conformable, the above description diverges slightly from the original diagnosis of *Cincturasporites appendices* Hacquebard and Barss 1957. The latter authors evidently did not encounter specimens in which the projections are developed proximally as well as (and much more strongly and abundantly) on the distal surface. Furthermore, many of the Spitsbergen representatives possess projections in excess of the 'three to ten' stated by Hacquebard and Barss.

As discussed previously, *Cincturasporites* Hacquebard and Barss 1957 appears to be an unsatisfactory taxon of doubtful validity; certainly the 'overlap' diagnostic of the genus is recognizable in rather less than half of the specimens described above. On the other hand, the cingulate and conspicuously verrucate nature of the species is in accordance with *Lophozonotriletes* Naumova as emended by Potonié (1958, pp. 27–28).

*Previous records.* From Upper Mississippian coal of the South Nahanni River area, Northwest Territories, Canada (Hacquebard and Barss 1957).

*Lophozonotriletes variverrucatus* sp. nov.

Plate 91, figs. 6, 7; text-fig. 10c

*Diagnosis.* Spores radial, trilete; amb convexly subtriangular, finely dentate to almost smooth. Laesurae distinct, simple, straight or slightly sinuous, almost attaining spore-body margin. Spore body usually somewhat lighter in colour than cingulum, which may show gradual, indistinct, equatorial decrease in thickness. Prominent distal sculpture of verrucae and, less commonly, baculae, distributed rather irregularly on both spore body and cingulum. Projections usually discrete, but bases sometimes fused, particularly around inner margin of cingulum; reduced or absent on equatorial region. Projections rather variable in size, shape, and disposition; range  $1\text{--}7\ \mu$  long,  $2\text{--}12\ \mu$  broad. Proximal hemisphere laevigate or infrapunctate.

*Dimensions* (30 specimens). Overall equatorial diameter  $42\text{--}68\ \mu$  (mean  $55\ \mu$ ); diameter of spore body  $23\text{--}36\ \mu$  (mean  $30\ \mu$ ); width of cingulum  $9\text{--}16\ \mu$  (mean  $12\ \mu$ ).

*Holotype.* Preparation P175/3, 48-6 94-0. L.1191.

*Locus typicus.* Citadellet (sample G1450), Spitsbergen; Lower Carboniferous.

*Description.* Holotype  $56\ \mu$  overall, diameter of spore body  $34\ \mu$ , width of cingulum  $11\ \mu$ ; proximal surface of spore body infrapunctate, of cingulum laevigate; whole distal hemisphere, excepting outer margin of cingulum, bearing numerous verrucae, some

baculae; sculpturing elements 2–7  $\mu$  long, 2–12  $\mu$  broad, frequently fused at bases in vicinity of spore body/cingulum junction; equatorial margin practically smooth.

*Remarks.* This cingulate species is included within *Lophozonotriletes* on the basis of its conspicuously developed verrucate/baculate sculpture. It is distinct from *L. rari-tuberculatus* (Luber), which has less numerous, more regular distal projections.

### Genus MONILOSPORA (Hacquebard and Barss) Staplin 1960

*Type species.* *M. moniliformis* Hacquebard and Barss 1957.

*Discussion.* The emendation of the genus *Monilospora* Hacquebard and Barss 1957 by Staplin (1960, p. 28) is here accepted, since it somewhat clarifies the morphological features, particularly in light of the effects of corrosion. The present writer is in agreement with Staplin's statement that three of the species in Hacquebard and Barss 1957—*Monilospora moniliformis*, *Tendosporites subcrenatus* (non Waltz), and *Densosporites subseratus*—perhaps represent different manifestations, due to variable preservation, of the same species.

It seems unfortunate that the terms 'capsula' and 'patella' introduced and utilized by Staplin (1960) in relation to the structure of this and other genera (*Monilospora*, *Tendosporites*) are not illustrated or defined in any detail, and are without reference to the layers of the spore wall; in their present form the use of such terms would only add to the confusion at present prevailing in palynological terminology. As understood by the present writer, Staplin's 'outer hull' or 'capsula' in fact refers to the envelopment of the intexine by the exoexine, which may be equatorially expanded and/or thickened, whereas 'patella' (cf. 'patina' of *Tholiosporites* Butterworth and Williams 1958, pp. 381–2; text-fig. 3) implies predominantly distal thickening of the exoexine.

*Affinity.* Unknown.

#### *Monilospora trimgensis* sp. nov.

Plate 92, figs. 2, 3

*Diagnosis.* Spores radial, trilete; amb subtriangular. Laesurae distinct, simple, straight, length approximately three-quarters to four-fifths spore-body radius. Spore body laevigate; subtriangular with broadly rounded apices and concave to almost straight sides. Broad cingulum showing gradual and slight equatorial decrease in thickness which is emphasized by corrosion; irregularly scalloped in outer part. Scalloping may be confined to outermost region or, if coarser, may extend about half-way towards spore-body margin.

*Dimensions* (30 specimens). Overall equatorial diameter 80–117  $\mu$  (mean 97  $\mu$ ); diameter of spore body 38–66  $\mu$  (mean 52  $\mu$ ).

*Holotype.* Preparation P145B/36, 38.0 100.9. L.1194.

*Locus typicus.* Triungen (sample G1466), Spitsbergen; Lower Carboniferous.

*Description.* Holotype 92  $\mu$  overall; cingulum width 19  $\mu$ , outer margin almost entirely scalloped (indented as much as 10  $\mu$ ), otherwise laevigate; spore body 53  $\mu$  in diameter, laevigate. The species is characterized by its large size and distinctive cingulum.



It is possible that the often highly irregular, scallop-like indentations of the cingulum are the result of corrosive action. However, it is important to note in this connexion that the other microfloral elements, contained in both samples (G1466, G636) from which *Monilospora triungensis* sp. nov. has been recovered, appear exceptionally well preserved.

*Comparison.* This species resembles *Monilospora mutabilis* Staplin 1960 (p. 28; p. 6, figs. 1–7, 9) but is consistently larger.

*Monilospora dignata* sp. nov.

Plate 92, figs. 4, 5

*Diagnosis.* Spores radial, trilete; amb subtriangular to oval. Laesurae distinct, simple, straight, length almost equal to body radius. Spore body subtriangular with straight to convex sides and rounded apices; laevigate to infrapunctate. Cingulum of somewhat variable width (mean  $14\ \mu$ ); including well-defined, continuous, thickened equatorial region, which is elevated, rounded in cross-section, and superficially either laevigate or finely wrinkled; width of marginal thickening typically variable on any given specimen, about  $5\text{--}10\ \mu$ . Cingulum otherwise smooth.

*Dimensions* (30 specimens). Overall equatorial diameter  $48\text{--}64\ \mu$  (mean  $56\ \mu$ ); diameter of spore body  $25\text{--}36\ \mu$  (mean  $30\ \mu$ ).

*Holotype.* Preparation P145B/18, 41.0 101.4. L.1197.

*Locus typicus.* Triungen (sample G1466), Spitsbergen; Lower Carboniferous.

*Description.* Holotype  $62\ \mu$  overall; laesurae almost attain spore-body margin; body laevigate, subtriangular with straight to convex sides; cingulum  $12\text{--}17\ \mu$  broad; prominent, elevated, smooth, marginal thickening ( $5\text{--}9\ \mu$  in width) appearing to encroach irregularly upon undifferentiated inner part of cingulum.

*Comparison.* *Monilospora dignata* sp. nov. is distinguishable from *M. moniliformis* Hacquebard and Barss 1957 (p. 38; pl. 5, figs. 8, 9) in possessing a smaller spore body, longer laesurae, and continuous marginal thickening. *Knoxisporites carnosus* (Knox) Butterworth and Williams 1958 (p. 369; pl. 2, figs. 8–10) is larger than *M. dignata* and its spore body is prescribed by a pronounced zone of cingulate thickening.

EXPLANATION OF PLATE 92

All figures  $\times 500$ , and from unretouched negatives.

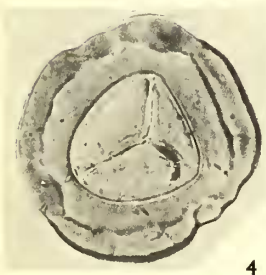
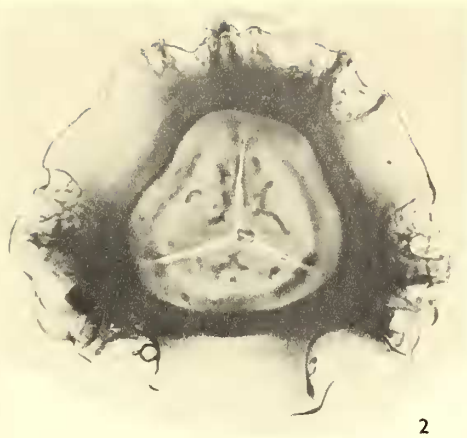
Fig. 1. *Cirratriradites solaris* Hacquebard and Barss 1957. Proximal surface; preparation P155/15, 40.3 102.8 (L.1206).

Figs. 2, 3. *Monilospora triungensis* sp. nov. 2, Proximal surface; preparation P145B/34, 34.0 108.5 (L.1195). 3, Holotype; proximal surface.

Figs. 4, 5. *Monilospora dignata* sp. nov. 4, Holotype; proximal surface. 5, Proximal surface; preparation P145B/1, 46.7 99.8 (L.1198).

Figs. 6, 7. *Cirratriradites elegans* (Waltz) Potonié and Kremp 1956. 6, Proximal surface; preparation P149A/41, 46.2 100.4 (L.1207). 7, Proximal surface; preparation P149A/2, 45.6 95.2 (L.1208).





PLAYFORD, Lower Carboniferous microspores



Infraturma PATINATI Butterworth and Williams 1958  
Genus THOLISPORITES Butterworth and Williams 1958

*Type species.* *T. scoticus* Butterworth and Williams 1958.

*Affinity.* Unknown.

*Tholisporites foveolatus* Hughes and Playford 1961

Plate 91, figs. 14, 15

*Dimensions* (75 specimens). Overall equatorial diameter 52–77  $\mu$  (mean 64  $\mu$ ); diameter of proximal central area 24–37  $\mu$  (mean 31  $\mu$ ).

*Comparison.* *Densosporites intermedius* (Waltz) comb. nov. shows some general resemblance, but is non-patinate and has different sculpture in the equatorial region.

Infraturma ZONATI Potonié and Kremp 1954  
Genus POTONIESPORES Artüz 1957

*Type species.* *P. bizonales* Artüz 1957.

*Discussion.* In her diagnosis of *Potoniespores*, Artüz (1957, p. 254) refers to the presence of a single V-shaped indentation of the equatorial margin. However, this feature may well prove merely a secondary (preservation) effect and hence its significance as a diagnostic characteristic is doubtful. Concise differentiation of the equatorial girdle into an inner thickened portion and an outer membranous zone permits the discrimination of *Potoniespores* from *Murospora* (al. *Simozonotriletes*).

*Affinity.* Unknown.

*Potoniespores delicatus* sp. nov.

Plate 91, figs. 12, 13

*Diagnosis.* Spores radial, trilete; amb subtriangular, conformable with spore-body outline. Laesurae distinct, simple, straight, length slightly less than spore-body radius. Spore body laevigate to infrapunctate; subtriangular with rounded apices and markedly concave to slightly convex sides. Equatorial girdle entirely laevigate; abruptly and uniformly differentiated into a prominent, dark, thickened, inner part and a thin, outer, diaphanous zone which is frequently folded and torn. Approximately half to two-thirds of the total girdle width is occupied by the inner thickened portion.

*Dimensions* (35 specimens). Overall equatorial diameter 50–69  $\mu$  (mean 58  $\mu$ ); diameter of spore body 23–33  $\mu$  (mean 27  $\mu$ ).

*Holotype.* Preparation P180B/4, 24·7 95·1. L.1202.

*Locus typicus.* Birger Johnsonfjellet (sample G1102), Spitsbergen; Lower Carboniferous.

*Description.* Holotype 54  $\mu$  overall; body concavely subtriangular, 24  $\mu$  in diameter, infrapunctate; equatorial girdle 15  $\mu$  broad, (inner) two-thirds occupied by dark, thickened portion, outer membranous zone with one conspicuous fold.

*Comparison.* *Potoniespores bizonales* Artüz 1957 (p. 254; pl. 6, fig. 47) differs from

*P. delicatus* sp. nov. in possessing longer laesurae and a relatively broader outer membranous zone. *Hymenozonotriletes concavus* Ishchenko 1956 (p. 63; pl. 12, fig. 134) has a much larger spore body together with somewhat irregular differentiation of the equatorial girdle.

Genus CIRRATRIRADITES Wilson and Coe 1940

*Type species.* *C. saturni* (Ibrahim) Schopf, Wilson, and Bentall 1944.

*Affinity.* Microspores showing close resemblance to *Cirratriradites anulatus* Kosanke and Brokaw (*in* Kosanke 1950) have been recovered from the herbaceous, heterosporous lycopod *Selaginellites suissei* Zeiller (Chaloner 1954), and also from the detached, heterosporous strobilus *S. crassicinctus* Hoskins and Abbott (1956).

*Cirratriradites solaris* Hacquebard and Barss 1957

Plate 92, fig. 1

*Description of specimens.* Spores radial, trilete; amb convexly subtriangular, conformable with spore-body outline. Laesurae distinct, straight, length approximately equal to body radius; bordered by strongly developed lips individually 3–4  $\mu$  wide. Spore-body wall very thick (5–9  $\mu$ ), irregularly punctate to microreticulate. Membranous zona relatively thin, supported by numerous, radially disposed, anastomosing ribs, which tend to be emphasized by corrosion. Well-preserved specimens uncommon.

*Dimensions* (25 specimens). Overall equatorial diameter 117–252  $\mu$  (mean 189  $\mu$ ); diameter of spore body 55–100  $\mu$  (mean 78  $\mu$ ). This agrees closely with the combination of the size ranges observed by Hacquebard and Barss (1957) and Staplin (1960).

*Comparison.* *Hymenozonotriletes auranthiacus* Naumova (Ishchenko 1956, p. 67; pl. 13, fig. 144), recorded also as *Zonotriletes auranthiacus* (Naumova) Waltz (*in* Luber and Waltz 1938, p. 16; pl. 3, fig. 40), is undoubtedly a closely related species. It is distinguishable from *C. solaris* in its smaller size and in possessing shorter, indistinct, apparently simple laesurae.

*Previous records.* This species has been reported previously from the Upper Mississippian of Canada (Hacquebard and Barss 1957; Staplin 1960).

*Cirratriradites elegans* (Waltz) Potonié and Kremp 1956

Plate 92, figs. 6, 7

1938 *Zonotriletes elegans* Waltz *in* Luber and Waltz, p. 15; pl. 3, fig. 32.

1956 *Cirratriradites elegans* (Waltz) Potonié and Kremp, p. 126.

1958 *Hymenozonotriletes elegans* (Waltz) Ishchenko, p. 67; pl. 7, fig. 88.

*Description of specimens.* Spores radial, trilete; amb convexly subtriangular, conformable with spore-body outline. Laesurae distinct, straight; extending on to zona, frequently reaching equator; accompanied by conspicuous, smooth, elevated, thickened lips, having maximum development on spore body, extending 4–6  $\mu$  on either side of laesurae. Spore body scabrate; non-foveolate. Zona much lighter in colour than spore body, more or less smooth, often folded, shows equatorial decrease in thickness; radially pitted or channelled in corroded specimens.



*Dimensions* (45 specimens). Overall equatorial diameter 70–128  $\mu$  (mean 102  $\mu$ ); diameter of spore body 44–63  $\mu$  (mean 53  $\mu$ ).

*Previous records.* *Cirratiradites elegans* has been known hitherto only from the U.S.S.R. Waltz (*in* Lubert and Waltz 1938) described it initially from Viséan strata of the Moscow Basin, and a recent report is from Viséan to Namurian rocks of the Dnieper–Donetz Basin (Ishchenko 1958).

### Genus CAMPTOZONOTRILETES Staplin 1960

*Type species.* *C. vermiculatus* Staplin 1960.

*Affinity.* Unknown.

### *Camptozonotriletes velatus* (Waltz) comb. nov.

Plate 93, figs. 1–3

1938 *Zonotriletes velatus* Waltz *in* Lubert and Waltz, p. 14; pl. 3, fig. 35, and pl. A, fig. 18.

1955 *Reticulatisporites velatus* (Waltz) Potonié and Kremp, p. 112.

1958 *Hymenozonotriletes velatus* (Waltz) Ishchenko, p. 75; pl. 8, fig. 105.

*Description of specimens.* Spores radial, trilete; amb roundly subtriangular to sub-circular. Laesurae distinct, straight, equal to or slightly less than body radius; simple, or bordered by narrow, thickened, elevated lips which often extend, and diverge markedly, immediately beyond radial termini of laesurae, thus appearing rather ‘spanner-like’ in polar view. Equatorial zone (‘flange’) uniform, lighter in colour than spore body; outer margin smooth or undulating (due to folding), more or less conformable with spore-body equator. Distal surface marked by development of a variable number of dark, thickened ridges of irregular length and disposition, particularly characteristic of spore body but often extending on to zona. Ridges 4–8  $\mu$  wide, simple or divided equally by a narrow longitudinal channel; sometimes connected to form an irregular, wide-meshed reticulum; rarely present on proximal surface.

*Dimensions* (100 specimens). Overall equatorial diameter 57–116  $\mu$  (mean 84  $\mu$ ); diameter of spore body 33–88  $\mu$  (mean 57  $\mu$ ). This extends considerably the size ranges quoted by Waltz (*in* Lubert and Waltz 1938) and Ishchenko (1958).

*Remarks.* The spores described above occur abundantly in the upper horizons of the Lower Carboniferous of Spitsbergen; they conform closely to the descriptions given by Waltz (*in* Lubert and Waltz 1938) and by Ishchenko (1958) of respectively *Zonotriletes velatus* and *Hymenozonotriletes velatus*. The assignment of the species to *Reticulatisporites* (Ibrahim) by Potonié and Kremp (1955, p. 112) is clearly incorrect. It is here included within *Camptozonotriletes* Staplin 1960 on the basis of structure (spore with an equatorial flange) and prominent distal sculpture (irregular muri).

*Previous records.* *Camptozonotriletes velatus* (Waltz) comb. nov. has been recorded hitherto exclusively from the U.S.S.R. Lubert and Waltz (1938, 1941) report its occurrence in Lower Carboniferous strata of the Moscow Basin and Selizharovo and Voronezh regions. According to the work of Ishchenko (1958) the species is present in Upper Devonian and Viséan rocks of the Dnieper–Donetz Basin, but apparently absent in the Tournaisian.

Genus *DIATOMOZONOTRILETES* (Naumova) emend.

1939 *Diatomozonotriletes* Naumova, p. 355; fig. 1.

1956 *Reinschospora* Schopf, Wilson, and Bentall,  $\beta$  section *Diatomozonotriletes* (Naumova) Potonié and Kremp, pp. 131–2.

1961 *Diatomozonotriletes* (Naumova) Potonié and Kremp 1956; Hughes and Playford, p. 40.

*Emended diagnosis.* Microspores radial, trilete; spore body triangular or subtriangular in equatorial outline. Laesurae usually well defined and long; simple or accompanied by lips. Spore body almost entirely encompassed by prominent zona (corona) consisting of numerous, strongly developed, mainly discrete saetae (fimbriae) emanating radially from equatorial margin of spore body. Saetae are particularly well developed in central interradianal equatorial regions, characteristically exhibiting a gradual diminution in size towards the triangular apices of the spore, where they may be either absent or considerably reduced. Saetae pointed or blunt; sometimes fused, at least in part, but always remain recognizable individually within the corona as distinct structural entities. Spore body often sculptured, particularly on distal surface.

*Type species* (here designated). *Diatomozonotriletes saetosus* (Hacquebard and Barss 1957, p. 41; pl. 6, fig. 3) Hughes and Playford 1961.

*Other species.* The following species are now included within *Diatomozonotriletes* (Naumova) emend.

1. *Diatomozonotriletes* (al. *Reinschospora*) *cervicornutus* (Staplin 1960, p. 24; pl. 5, figs. 1–3) comb. nov. Occurrence: Canada (after Staplin 1960)—Golata formation, Alberta; Upper Mississippian.

2. *Diatomozonotriletes* (al. *Zonotriletes*) *curiosus* (partim) (Waltz in Luber and Waltz 1938, pl. 4, fig. 49; non pl. A, fig. 13) Ishchenko 1956. Occurrence: U.S.S.R. (after Luber and Waltz 1941)—Moscow Basin, Kizel, Selizharovo, and Voronezh regions; Lower Carboniferous. U.S.S.R. (after Ishchenko 1956, 1958)—western Donetz Basin, Dnieper–Donetz Basin; Viséan.

3. *Diatomozonotriletes hughesii* sp. nov.

4. *Diatomozonotriletes* (al. *Reinschospora*) *jubatus* (Staplin 1960, p. 23; pl. 5, figs. 7, 8) comb. nov. Occurrence: Canada (after Staplin 1960)—Golata formation, Alberta; Upper Mississippian.

5. *Diatomozonotriletes* (al. *Reinschospora*) *nahannensis* (Hacquebard and Barss 1957, p. 41; pl. 6, figs. 1, 2) comb. nov. Occurrence: Canada (after Hacquebard and Barss 1957)—South Nahanni River area, Northwest Territories; Upper Mississippian.

6. *Diatomozonotriletes* (al. *Reinschospora* sect. *Diatomozonotriletes*) *radforthi* (Potonié 1956, p. 69; pl. 9, fig. 90) comb. nov. Occurrence: Canada (after Radforth and McGregor 1954, p. 605)—Wabumun Lake; age uncertain (see Radforth and McGregor 1956, footnote on pp. 27–28).

7. *Diatomozonotriletes rarus* sp. nov.

8. *Diatomozonotriletes trilinearis* sp. nov.

9. *Diatomozonotriletes ubertus* Ishchenko 1956, p. 100; pl. 19, fig. 242. Occurrence: U.S.S.R. (after Ishchenko 1956, 1958)—western Donetz Basin, Dnieper–Donetz Basin; Viséan to Lower Namurian.

10. *Diatomozonotriletes* (al. *Zonotriletes*) *vesicarius* (Waltz in Luber and Waltz 1941, p. 30; pl. 5, fig. 78) comb. nov. Occurrence: U.S.S.R. (after Luber and Waltz 1941)—Selizharovo region; Lower Carboniferous.

*Discussion.* In anticipation of the possible eventual recognition of *Diatomozonotriletes* Naumova as a distinct form-genus, Potonié and Kremp (1956a, pp. 131–2) proposed its subgeneric ('sectional') status within the category of *Reinschospora* Schopf, Wilson, and Bentall. Subsequently, Hughes and Playford (1961) incorrectly attributed generic rank to *Diatomozonotriletes* (Naumova) Potonié and Kremp 1956 (in Potonié 1956, p. 69), which lacks the designation of a type species.

Species recorded recently (by Ishchenko 1956, 1958; Hacquebard and Barss 1957; Staplin 1960; Hughes and Playford 1961), together with those described below, indicate the consistent presence in the Lower Carboniferous of a distinct group of *Reinschospora*-like spores possessing coronae of relatively coarse, strongly developed saetae. On the other hand, Upper Carboniferous representatives of

*Reinschospora*, for example the type species *R. speciosa* (Loose), are characterized by more delicate coronae consisting of a dense aggregation of much finer fimbriae. Such, indeed, is the criterion upon which Potonié and Kremp (1956a) based their sectional subdivision of *Reinschospora*. Thus the separation of *Diatomozonotriletes* from *Reinschospora* is warranted on morphographical grounds and appears also to have definite stratigraphical significance.

*Comparison.* Some species of *Anapiculatisporites* Potonié and Kremp 1954, for example *A. serratus* sp. nov., possess a strongly spinose equatorial margin which may simulate the zona of *Diatomozonotriletes*. In such cases, however, the sculpture visible at the margin represents an equatorial development of the predominantly distal, spinose sculpture of *Anapiculatisporites*. In *Diatomozonotriletes*, distal sculpture is subordinate and quite distinct from the structural components of its encompassing zona.

The present writer is in agreement with Potonié (1960, p. 60) concerning the 'problematical' nature of *Procoronaspora* Butterworth and Williams 1958. This genus appears to overlap the connotations of several previously instituted genera, such as *Lycospora*, but future work may possibly justify its recognition as a discrete form-genus. *Procoronaspora* is undoubtedly closely related to *Diatomozonotriletes* (Naumova) emend., but the 'fine grade' of its diverse sculpture ('grains, verrucae, spines, baculae, &c.') serves to distinguish it from the latter genus. As noted by Potonié (1960, p. 60), Butterworth and Williams's assignment of *Diatomozonotriletes curiosus* (Waltz) is incorrect.

*Affinity.* Unknown.

#### *Diatomozonotriletes saetosus* (Hacquebard and Barss) Hughes and Playford 1961

Plate 93, figs. 4–7

1938 *Zonotriletes speciosus* (non Loose) Waltz in Lubert and Waltz, pp. 14–15; pl. 4, fig. 48, and pl. A, fig. 9.

1956 *Diatomozonotriletes speciosus* (non Loose) Ishchenko, pp. 99–100; pl. 19, figs. 239–41.

1957 *Reinschospora saetosus* Hacquebard and Barss, pp. 41–42; pl. 6, fig. 3.

1961 *Diatomozonotriletes saetosus* (Hacquebard and Barss) Hughes and Playford, p. 40; pl. 4, figs. 14, 15.

*Description of specimens.* Spores radial, trilete; spore body subtriangular with concave sides and rounded to truncated apices. Laesurae distinct, straight, extending almost to equatorial margin; simple or bordered by narrow, slightly thickened lips. Prominent corona comprising nine to fifteen discrete, typically pointed saetae projecting laterally from each interradian portion of the spore-body equator. Saetae 2.5–5  $\mu$  broad at base, 3–22  $\mu$  long; attain maximum length in central interradian region, diminishing uniformly towards smooth triangular apices. Spore body usually entirely laevigate, occasionally finely granulate on distal surface. Exine thick (2–4  $\mu$ ), often distinctly thinner at apices.

*Dimensions* (85 specimens). Equatorial diameter of spore body 36–63  $\mu$  (mean 49  $\mu$ ).

*Holotype.* As designated by Hacquebard and Barss (1957, p. 42).

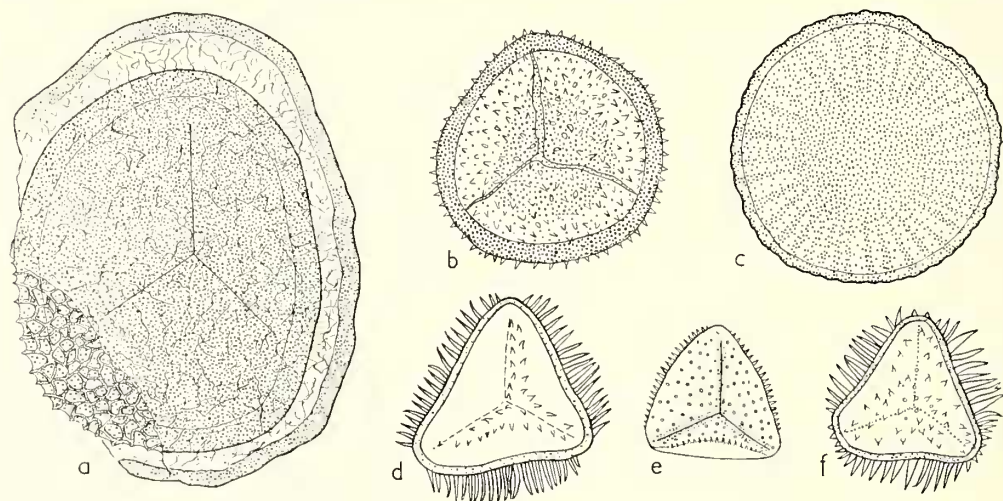
*Locus typicus.* South Nahanni River area, Northwest Territories, Canada (after Hacquebard and Barss 1957); Upper Mississippian.

*Previous records.* *Diatomozonotriletes saetosus* has been recorded extensively from the U.S.S.R., as follows: Lower Carboniferous of the Moscow Basin and of the Selizharovo, Borovichi, and Kizel regions (Lubert and Waltz 1938, 1941); Lower Viséan only of the



western Donetz Basin (Ishchenko 1956); Lower Carboniferous of the Melekess and Busuluk deep wells (Byvsheva 1957); Viséan–Namurian of the Dnieper–Donetz Basin (Ishchenko 1958); Yasnopolyansky substage (Lower Viséan) of the Saratov–Stalingrad Volga area (Loginova 1959); and Lower Carboniferous of the Volga–Ural region (Byvsheva 1960). Note that these Russian authors invariably incorrectly assign this species to Loose's species, i.e. *Reinschospora speciosa* (Loose) Schopf, Wilson, and Bental.

Hacquebard and Barss (1957) described the species from the Upper Mississippian of



TEXT-FIG. 11. Camera lucida drawings; all magnifications  $\times 500$ . *a*, *Velosporites microreticulatus* sp. nov.; proximal surface; preparation P163/7, 49.6–110.7 (L.1236). *b*, *Spinozonotriletes balteatus* sp. nov.; proximal surface; preparation P149A/3, 42.4–105.8 (L.1244). *c*, *Radialetes costatus* gen. et sp. nov.; preparation P159/5, 48.0–112.5 (L.1252). *d*, *Diatomozonotriletes trilinearis* sp. nov.; distal surface; preparation P149A/2, 26.9–108.5 (L.1227). *e*, *D. rarus* sp. nov.; distal surface; preparation P145B/2, 43.6–110.9 (L.1230). *f*, *D. hughesii* sp. nov.; distal surface; preparation P149B/1, 44.6–104.5 (L.1223).

Canada (see above), and Hughes and Playford (1961) reported some specimens from the Lower Carboniferous (sample B609) of Spitsbergen.

*Diatomozonotriletes hughesii* sp. nov.

Plate 93, figs. 8–11; text-fig. 11f

*Diagnosis.* Spores radial, trilete; amb subtriangular with rounded apices and concave to almost straight sides. Laesurae perceptible to distinct, simple, more or less straight, almost attaining equatorial margin. Well-developed corona consisting of eleven to seventeen large, mutually dissociated, uniformly tapering saetae projecting laterally from each side of the triangular amb, and having pointed, rarely divided apices. Saetae reach maximum size on centres of sides (up to  $16\ \mu$  long and  $4\ \mu$  in basal diameter); absent or commonly reduced to small coni on triangular apices of spore body. Distal surface of spore body distinctly echinate, bearing scattered, somewhat irregularly distributed

spines (length  $2-6\ \mu$ ); bases of spines rather bulbous (diameter  $1-2\ \mu$ ). Proximal surface laevigate. Exine  $1.5-2\ \mu$  thick.

*Dimensions* (80 specimens). Equatorial diameter of spore body  $30-47\ \mu$  (mean  $39\ \mu$ ).

*Holotype*. Preparation P149B/1, 47.3 107.6. L.1218.

*Locus typicus*. Triungen (sample G1470), Spitsbergen; Lower Carboniferous.

*Description*. Holotype body diameter  $46\ \mu$ ; saetae (interradial)  $5-15\ \mu$  long; triangular apices of amb each bearing four to five coni,  $2-3\ \mu$  long,  $1.5\ \mu$  broad at base; distal spinae congregated in polar region, relatively sparse elsewhere, average length  $5\ \mu$ ; exine  $2\ \mu$  thick. This species is characterized by distinctly echinate distal sculpture, together with frequent development of small coni on the radial corners of the spore body.

*Comparisou*. *Diatomozonotriletes curiosus* (Waltz) Ishchenko (1956, pp. 100-1; pl. 19, fig. 243) and '*Reinschospora* sp. A' of Staplin (1960, p. 24; pl. 5, fig. 18) have finer, more numerous saetae.

*Diatomozonotriletes trilinearis* sp. nov.

Plate 93, figs. 12-14; text-fig. 11d

*Diagnosis*. Spores radial, trilete; amb subtriangular with straight to slightly concave sides, and rounded to truncated apices. Laesurae distinct, simple, straight, almost reaching equatorial margin. Seventeen to twenty-six closely spaced saetae project radially from sides of spore body amb constituting prominent corona, which is not developed at triangular apices. Saetae pointed, occasionally divided, mutually dissociated, basal diameter  $1.5-2\ \mu$ , longest in central interradian region (up to  $14\ \mu$ ), exhibiting a slight, gradual reduction in size towards smooth apices of spore body. Distal surface bearing sharply tapered spinae,  $2-4\ \mu$  long,  $1.5-2\ \mu$  broad at base, characteristically congregated in a Y-shaped area, the orientation and radial extent of which conforms with that of the trilete mark on the opposite surface. Each limb of the 'Y' often consists of two parallel lines of spinae. Apart from this restricted spinose sculpture, spore body laevigate. Exine  $1.5-2.5\ \mu$  thick.

*Dimensions* (45 specimens). Equatorial diameter of spore body  $35-56\ \mu$  (mean  $45\ \mu$ ).

*Holotype*. Preparation P149A/2, 33.5 95.6. L.1224.

*Locus typicus*. Triungen (sample G1470), Spitsbergen; Lower Carboniferous.

*Description*. Holotype body diameter  $50\ \mu$ ; coronal saetae  $4-13\ \mu$  long, less than  $1\ \mu$  apart; constituent spinae of Y-shaped, distal, sculptured area are less closely spaced in polar region.

*Comparison*. Type 63 of Reinsch (1884, p. 7; pl. 2, fig. 27) from the Russian (?Lower) Carboniferous may be conspecific with *Diatomozonotriletes trilinearis* sp. nov.

*Diatomozonotriletes rarus* sp. nov.

Plate 93, figs. 15, 16; text-fig. 11e

*Diagnosis*. Spores radial, trilete; amb subtriangular with slightly convex to slightly concave sides and rounded apices. Laesurae distinct, straight, length three-quarters of,

to almost equal to, spore-body radius; bordered by thickened, slightly elevated lips, individually about  $2\mu$  wide. Equatorial corona consisting of discrete, closely spaced, pointed saetae attaining maximum size interradially ( $3.5\text{--}5\mu$  long,  $1.5\text{--}2\mu$  in basal diameter) and diminishing gradually and uniformly towards the smooth triangular apices. Proximal surface of spore body laevigate; distal surface echinate, with numerous, small, fairly evenly distributed coni,  $1.5\text{--}2\mu$  long,  $1\text{--}1.5\mu$  broad at base, and  $1.5\text{--}4\mu$  apart. Exine (excluding sculpture) up to  $1\mu$  thick.

*Dimensions* (15 specimens). Equatorial diameter of spore body  $37\text{--}48\mu$  (mean  $42\mu$ ).

*Holotype*. Preparation P145B/19, 38.3 103.4. L.1228.

*Locus typicus*. Triungen (sample G1466), Spitsbergen; Lower Carboniferous.

*Description*. Holotype body diameter  $39\mu$ ; distal coni reduced in size and density in equatorial region; laesurae conspicuously labiate. This distinctive but very rare species is characterized by relatively short, pointed, equatorial saetae, distal echinate sculpture, together with marked lip development.

*Comparison*. *Diatomozonotriletes rarus* sp. nov. is similar to *D. curiosus* (Waltz in Lubert and Waltz 1938, pl. 4, fig. 49) Ishchenko 1956, which is distinguishable, however, in possessing longer saetae and simple laesurae.

Anteturma POLLENITES R. Potonié 1931

Turma SACCITES Erdtman 1947

Subturma MONOSACCITES (Chitaley) Potonié and Kremp 1954

Infraturma TRILETESACCITI Leschik 1955

Subinfraturma INTRORNATI Butterworth and Williams 1958

*Discussion*. Butterworth and Williams's (1958) suprageneric subdivision of monosaccate grains on the basis of predominantly either internal or external sculpture is

#### EXPLANATION OF PLATE 93

All figures  $\times 500$ , and from unretouched negatives.

Figs. 1–3. *Camptozonotriletes velatus* (Waltz) comb. nov. 1, Proximal surface; preparation P164/15, 32.2 101.5 (L.1210). 2, Distal surface; preparation P149A/27, 38.7 104.4 (L.1211). 3, Proximal surface; preparation P157/4, 23.6 113.6 (L.1212).

Figs. 4–7. *Diatomozonotriletes saetosus* (Hacquebard and Barss) Hughes and Playford 1961. 4, Proximal surface; preparation P167B/10, 35.9 104.0 (L.1215). 5, Proximal surface; preparation P167B/4, 35.5 100.7 (L.1214). 6, Proximal surface; preparation P167A/2, 25.3 110.3 (L.1216). 7, Proximal surface; preparation P127/3, 53.7 96.9 (L.1217).

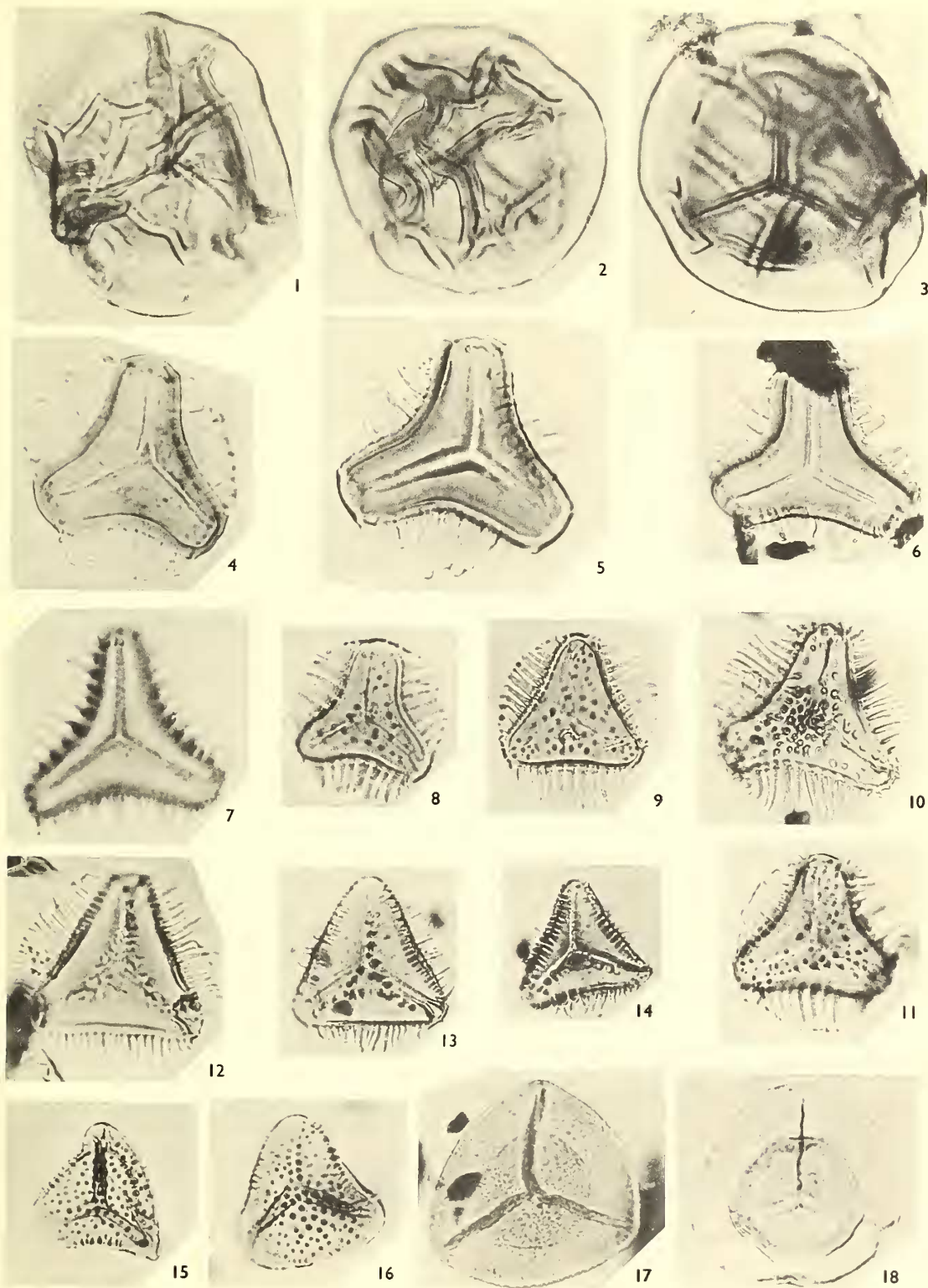
Figs. 8–11. *Diatomozonotriletes hughesii* sp. nov. 8, Proximal surface; preparation P149A/1, 28.2 113.3 (L.1219). 9, Proximal surface; preparation P149A/35, 32.7 102.0 (L.1220). 10, Holotype; distal surface. 11, Distal surface; preparation P157/2, 18.9 108.5 (L.1222).

Figs. 12–14. *Diatomozonotriletes trilinearis* sp. nov. 12, Holotype; proximal surface. 13, Distal surface; preparation P149B/1, 15.5 99.8 (L.1225). 14, Proximal surface; preparation P149B/2, 38.5 97.4 (L.1226).

Figs. 15, 16. *Diatomozonotriletes rarus* sp. nov. 15, Holotype; proximal surface. 16, Distal surface; preparation P145C/1, 30.3 106.6 (L.1229).

Figs. 17, 18. *Endosporites micromanifestus* Hacquebard 1957. 17, Proximal surface; preparation P145B/2, 24.5 94.3 (L.1232). 18, Proximal surface; preparation P174/2, 25.5 112.0 (L.1231).







undoubtedly of morphographical significance. However, in many cases the distinction is not readily ascertainable. Although Butterworth and Williams (1958) assigned their genus *Remysporites* to the Extrornati, Potonié (1960, p. 72) included it within the Intrornati since he considered that the often 'externally microreticulate' bladder appearance of this genus may well be due to the development of infrareticulate structure rather than to external sculpture of the exoexine. According to Potonié similar manifestation of internal bladder structure is evident in other genera (*Endosporites*, *Wilsonia*, *Guthörlisporites*, *Microsporites*). Hence, *Velosporites* Hughes and Playford 1961, which shows 'fine external sculpture' of the saccus, is also probably more correctly included within the Intrornati.

#### Genus ENDOSPORITES Wilson and Coe 1940

*Type species.* *E. ornatus* Wilson and Coe 1940.

*Discussion.* Richardson (1960, p. 49) has with justification drawn attention to the overlapping connotations of *Auroraspora* Hoffmeister, Staplin, and Malloy 1955 and *Endosporites* Wilson and Coe 1940. However, Richardson's statement that *Auroraspora* 'differs from *Endosporites* in the absence of a limbus' is questionable, since the original diagnosis of the latter genus (Wilson and Coe 1940, p. 184), which is still accepted unemended, and a recent morphological amplification of the type species (Wilson 1960) contain no reference to an equatorial bladder thickening (limbus). Admittedly, some authors (Potonié and Kremp 1954; Bhardwaj 1957; Chaloner 1953*a*, 1958*b*) have noted the characteristic presence of a limbus in representatives of *Endosporites*, and it is undoubtedly an important morphographical feature which may well have generic significance. However, there are many species included within *Endosporites*, and presently recognized as such, which appear to lack the development of a limbus. In all, therefore, a complete reappraisal of the type species of this and other related monosaccate genera (particularly *Auroraspora*) would seem advisable. Pending this, the present writer considers it preferable at this stage to retain the original generic assignment of the two species instituted by Hacquebard (1957), *E. micromanifestus* and *E. macromanifestus*, both of which Richardson (1960) transferred to *Auroraspora*.

Perhaps the least unsatisfactory distinction between *Auroraspora* and *Endosporites* was expressed by Hoffmeister, Staplin, and Malloy (1955*b*, p. 381) on the basis of relative thicknesses of bladder and body walls. According to these authors *Auroraspora* possesses a central body having a 'moderately thick wall' enclosed by a 'transparent and very thin bladder'; whereas in *Endosporites* the body wall 'approximates the bladder in thickness' (cf. Wilson 1960, pl. 1, fig. 5—explanation p. 31). As Richardson (1960, p. 49) implies, little diagnostic importance can be attached to actual or relative colour which is partially dependent upon preservation and maceration procedures.

Wilson (1960) has demonstrated conclusively that in *Endosporites ornatus* the central body is attached to the bladder on the proximal side only; this method of attachment was interpreted earlier by Potonié and Kremp (1954, p. 149; fig. 81).

*Affinity.* Chaloner (1953*a*, 1958*b*) has reported the occurrence of microspores very similar to *Endosporites globiformis* (Ibrahim) Schopf, Wilson, and Bentall 1944 in the lycopod cone *Polysporia mirabilis* Newberry 1873 (syn. *Lepidostrobus zea* Chaloner 1953*a*). Earlier, Schopf, Wilson, and Bentall (1944, p. 45) stated that '*Endosporites* is



related to some of the Pennsylvanian Cordaitaleans' because of the presence of *E. pelucidus*-type spores within the strobilus *Cordaianthus shuleri* Darrah 1940. This attribution of *Endosporites* has been discounted by Wilson (1960, p. 31) because he has shown that *E. pelucidus* is more correctly assigned to the genus *Florinites* (see Wilson 1958).

*Endosporites micromanifestus* Hacquebard 1957

Plate 93, figs. 17, 18

1956 *Hymenozonotriletes* aff. *variabilis* Naumova; Ishchenko, p. 62; pl. 11, figs. 129, 130.

1957 *Endosporites micromanifestus* Hacquebard, p. 317; pl. 3, fig. 16.

1960 *Auroraspora micromanifestus* (Hacquebard) Richardson, p. 51.

*Description of specimens.* Spores radial, trilete; amb convexly subtriangular. Laesurae distinct, accompanied by elevated, rather irregular, flange-like lips that frequently extend to the equator. Central body thin, smooth, well defined; outline more or less conformable with amb. Bladder thin, often folded, infragranulate.

*Dimensions* (50 specimens). Overall equatorial diameter 42–95  $\mu$  (mean 67  $\mu$ ); diameter of central body 28–65  $\mu$  (mean 44  $\mu$ ).

*Previous records.* Described initially by Hacquebard (1957) from lowermost Mississippian strata of Nova Scotia, this species has been recorded subsequently from the Scottish Viséan by Love (1960) and from one sample (B685) of the Lower Carboniferous of Spitsbergen (Hughes and Playford 1961). It evidently occurs also throughout the Tournaisian–Viséan–Namurian succession of the western extension of the Donetz Basin (Ishchenko 1956, p. 62).

Genus REMYSPORITES Butterworth and Williams 1958

*Type species.* *R. magnificus* (Horst) Butterworth and Williams 1958.

*Discussion.* Contrary to the statement of Butterworth and Williams (1958, p. 386), the saccus in this genus is now considered to envelop the central body entirely (see discussion herein of *Velosporites*).

*Affinity.* Affinity with the Cycadofilices is suggested by the similarity between the type species and the spores borne by *Paracalathiops stachei* (Stur) Remy 1953 (see Butterworth and Williams 1958, p. 387; Potonié 1960, p. 72).

*Remysporites albertensis* Staplin 1960

Plate 94, fig. 3

*Description of specimens.* Spores radial, trilete; amb and body outline subcircular to circular. Smooth central body completely enveloped by loosely fitting bladder; both commonly folded, and probably attached at conspicuous proximal polar (contact) area. Contact area convexly subtriangular, distinctly sculptured with mixed rugulae and verrucae; bladder surface otherwise smooth. Central body and bladder walls both thin (about 1–1.5  $\mu$ ). Laesurae distinct, simple, straight, length half to two-thirds central body radius.

*Dimensions* (25 specimens). Overall equatorial diameter 146–205  $\mu$  (mean 178  $\mu$ ); diameter of central body 113–150  $\mu$  (mean 130  $\mu$ ).

*Comparison.* The specimens conform closely with the diagnosis given by Staplin (1960, p. 35), except that they extend the size range considerably. However, Staplin does not state the number of specimens he measured, and in any case it seems likely that such large monosaccate species exhibit considerable size diversity, dependent probably upon mode of preservation and/or maceration (cf. Butterworth and Williams 1958, p. 388).

*Previous records.* From the Golata formation (Upper Mississippian) of Alberta, Canada (Staplin 1960).

### Genus VELOSPORITES Hughes and Playford 1961

*Type species.* *V. echinatus* Hughes and Playford 1961.

*Discussion.* This genus includes large monosaccate spores (as diagnosed by Hughes and Playford 1961, p. 42) characterized by relatively minor but distinctive body-wall sculpture. It is also important to state that a limbus may or may not be present.

According to Butterworth and Williams (1958, p. 386) the genus *Remysporites* is characterized by 'bladder enveloping central body except on proximal side'; and it was principally on this basis that Hughes and Playford (1961) decided to erect the genus *Velosporites* to incorporate a species rather similar to *Remysporites magnificus* (Horst) Butterworth and Williams but possessing comprehensive bladder envelopment. Recently, however, through the courtesy of Drs. M. A. Butterworth and A. H. V. Smith of the National Coal Board, the opportunity has been taken of examining the material from which Butterworth and Williams diagnosed *Remysporites*. As a result the present writer came to the conclusion—jointly with Dr. Butterworth—that the bladder in *R. magnificus* (the type species) does, in fact, envelop the central body entirely. This is substantiated further by a more recently described representative of *Remysporites*, *R. albertensis* Staplin 1960 (p. 35; pl. 8, figs. 8, 10), which is also recorded herein. The characteristic sculpture and relatively thick wall of the central body, exhibited by the two species recorded below, is, however, considered sufficient to justify the continued recognition of *Velosporites* as a distinct form-genus.

*Affinity.* Unknown.

### *Velosporites echinatus* Hughes and Playford 1961

Plate 94, fig. 1

*Remarks.* The surface of the central body characteristically bears minute, sparsely distributed conical or very low, mound-like elevations, which are often evident only under oil immersion. The bladder is commonly folded on both large and small scale, the latter resulting in a microrugulate effect.

*Dimensions* (80 specimens). Overall equatorial diameter 102–194  $\mu$  (mean 140  $\mu$ ); diameter of central body 70–128  $\mu$  (mean 100  $\mu$ ).

*Velosporites microreticulatus* sp. nov.

Plate 94, fig. 2; text-fig. 11a

*Diagnosis.* Spores radial, trilete; monosaccate; amb circular to oval, more or less entire. Laesurae simple, straight, length approximately four-fifths central body radius, not evident on bladder. Central body distinct, circular to subcircular, thick-walled ( $4-9\ \mu$ ); distinct, finely reticulate sculpture of very narrow, pointed muri up to  $1.5\ \mu$  high, enclosing small, polygonal lumina which are  $1.5-7\ \mu$  broad (average  $3.5\ \mu$ ); surrounded completely by thin, transparent bladder. Bladder extending  $9-27\ \mu$  beyond central body margin; definite equatorial thickening (limbus)  $3-6.5\ \mu$  wide, smooth, imposing comparative rigidity to bladder. Bladder often densely microrugulate or vermiculate, frequently corroded or torn, thickness about  $0.5\ \mu$ .

*Dimensions* (16 specimens). Overall equatorial diameter  $100-140\ \mu$  (mean  $118\ \mu$ ); diameter of central body  $73-102\ \mu$  (mean  $88\ \mu$ ).

*Holotype.* Preparation P163/7, 22.3 94.7. L.1235.

*Locus typicus.* Birger Johnsonfjellet (sample G1089), Spitsbergen; Lower Carboniferous.

*Description.* Holotype  $120\ \mu$  overall, subcircular; central body  $92\ \mu$  in diameter,  $5\ \mu$  in thickness, circular, colour much darker than bladder; bladder partially removed thereby revealing detail of conspicuous microreticulate sculpture of central body; limbus  $6\ \mu$  wide.

Subturma POLYSACCITES Cookson 1947

Genus ALATISPORITES Ibrahim 1933

*Type species.* *A. pustulatus* Ibrahim 1933.

*Affinity.* Unknown.

*Alatisporites tessellatus* Staplin 1960

Plate 95, fig. 10

*Description of specimens.* Spores radial, trilete. Central body circular, finely and densely rugulate. Laesurae indistinct, simple, straight, length half to two-thirds body radius. Approximately seven to eight thin, overlapping, frequently strongly folded bladders are prominent equatorially but attached to distal surface of body.

*Dimensions* (17 specimens). Overall equatorial diameter  $75-109\ \mu$  (mean  $87\ \mu$ ); body diameter  $52-61\ \mu$  (mean  $56\ \mu$ ).

## EXPLANATION OF PLATE 94

All figures  $\times 500$ , and from unretouched negatives.

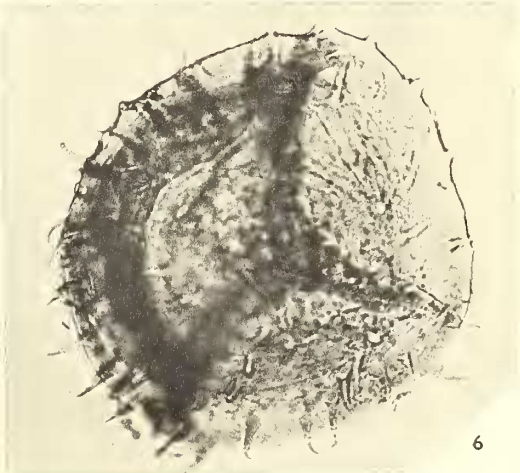
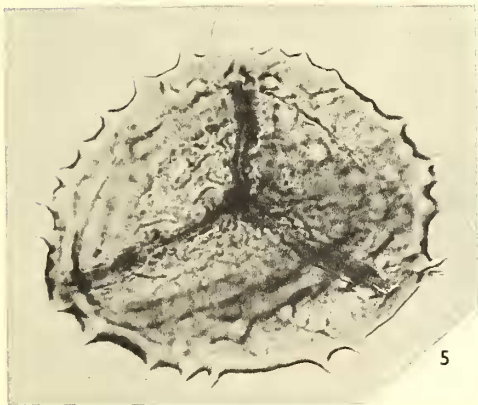
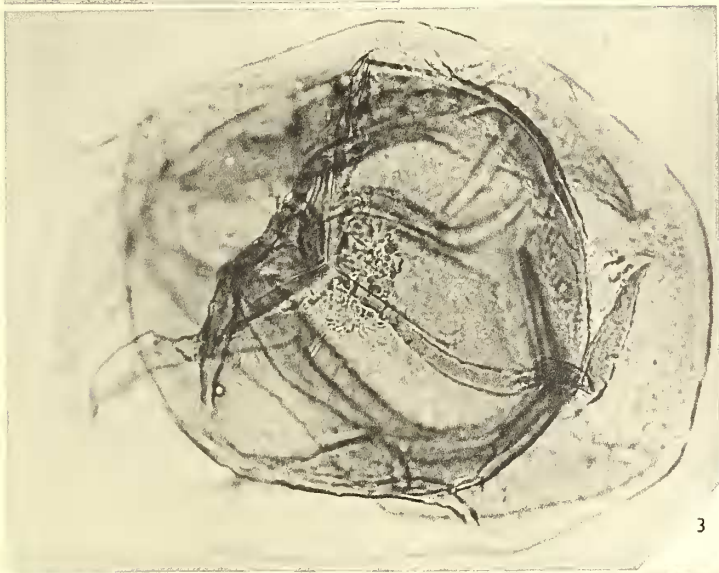
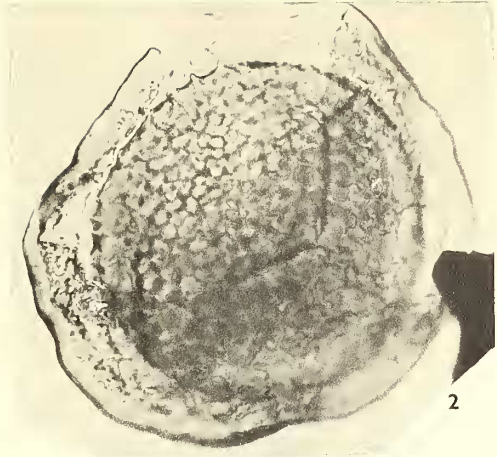
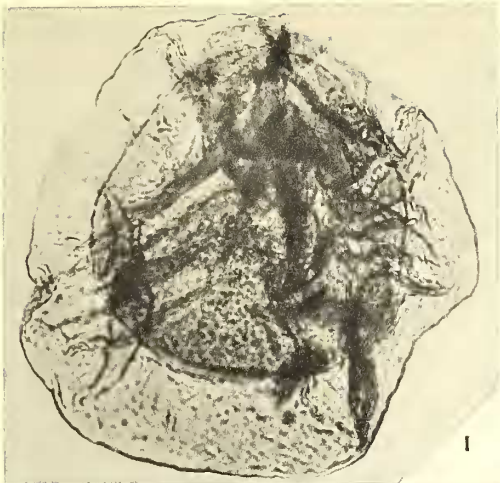
Fig. 1. *Velosporites echinatus* Hughes and Playford 1961. Proximal surface; preparation M811/5, 58.2 108.9 (L.1234).

Fig. 2. *Velosporites microreticulatus* sp. nov. Holotype; proximal surface.

Fig. 3. *Remysporites albertensis* Staplin 1960. Proximal surface; preparation P149A/15, 40.4 100.1 (L.1233).

Figs. 4-6. *Spinozonotriletes uncatatus* Hacquebard 1957. 4, Proximal surface; preparation P175/2, 42.8 108.9 (L.1238). 5, Proximal surface; preparation P148/5, 38.8 93.0 (L.1240). 6, Distal surface; preparation P148/51, 39.1 107.0 (L.1237).





PLAYFORD, Lower Carboniferous microspores





*Remarks.* Apart from extending the range of overall size, the Spitsbergen specimens conform very closely to the diagnosis given by Staplin (1960, p. 31; pl. 7, fig. 10).

*Previous records.* Described initially from the Golata formation (Upper Mississippian) of Alberta, Canada (Staplin 1960).

Turma ALETES Ibrahim 1933

Subturma AZONALETES (Luber) Potonié and Kremp 1954

Infraturma RETICULONAPITI (Erdtman) Vimal 1952

Genus RETIALETES Staplin 1960

*Type species.* *R. radforthii* Staplin 1960.

*Discussion.* In his diagnosis of this genus, Staplin (1960, p. 6) states: 'spores alete, but sometimes split along a few fine grooves that originate at one end and parallel the long axis'. Similar but usually more extensive splitting has been observed in certain Mesozoic microspores, e.g. *Schizosporis* Cookson and Dettmann 1959 and *Psophosphaera* Naumova (in Bolkhovitina 1959). In *Retialetes*, rupturing, when present, is always longitudinally situated, and suggests a possible mechanism for germination.

*Affinity.* Unknown.

*Retialetes radforthii* Staplin 1960

Plate 95, figs. 1-3

*Description of specimens.* Spores alete, ellipsoidal. Comprehensive reticulate sculpture comprised of rounded or flat-topped, low, smooth muri (1-3  $\mu$  high, 1-2.5  $\mu$  broad) enclosing subcircular to polygonal lumina 4-22  $\mu$  in longest diameter (usually about 8  $\mu$ ). Exine (excluding muri) 3-5  $\mu$  thick; often split along one, occasionally two or more, narrow grooves that parallel the long axis of the spore.

*Dimensions* (25 specimens). 102-182  $\mu$  (mean 144  $\mu$ ) by 66-107  $\mu$  (mean 84  $\mu$ ).

*Previous records.* This distinctive species was originally described by Staplin (1960) from the Upper Mississippian Golata formation of Alberta, Canada.

Genus RADIALETES gen. nov.

*Type species.* *R. costatus* sp. nov.

*Diagnosis.* Microspores radial, alete. Outline circular or subcircular. Distinctive sculpture consisting of radially disposed muri or incipient thickenings which thus give the spores an overall radiating appearance. Muri sometimes considerably diminished towards central portions of spores.

*Comparison.* The spore illustrated by Hoffmeister, Staplin, and Malloy (1955a, pl. 3, fig. 7) as '*Radiaspora*' sp. has similar, albeit exclusively distal, sculpture but differs from *Radialetes* gen. nov. in being distinctly trilete. As noted by Potonié (1956, p. 42), *Radiaspora* has yet to be validated as a generic name. *Radialetes* is distinct from *Aumancisporites* Alpern 1958 (p. 84), which is sculptured with more or less parallel grooves disposed transversely with respect to the long axis of the spore. *Undulatasporites* Leschik 1955 (p. 28) has irregular rugulate sculpture.

*Affinity.* Unknown.

*Radialetes costatus* sp. nov.

Plate 95, figs. 7-9; text-fig. 11c

*Diagnosis.* Spores radial, alete. Outline circular to subcircular; commonly distorted due to folding. Both surfaces sculptured with more or less distinct, low, non-anastomosing, radially disposed muri which attain maximum development at the margin, and may be lacking or considerably diminished centrally; muri  $1.5-5\ \mu$  broad,  $1-3\ \mu$  apart, up to  $2\ \mu$  high. Folding of exine usually results in marked apparent discordance of muri on opposing surfaces producing an overall 'cross-hatched' effect. Exine (including sculpture)  $2-6\ \mu$  thick; apart from muri, laevigate to finely granulate or punctate.

*Dimensions* (50 specimens). Diameter  $42-117\ \mu$  (mean  $70\ \mu$ ).

*Holotype.* Preparation P145B/38, 40.7 105.9. L.1249.

*Locus typicus.* Triungen (sample G1466), Spitsbergen; Lower Carboniferous.

*Description.* Holotype  $48\ \mu$ , circular; conspicuous radial muri  $1.5-3\ \mu$  broad,  $1-1.5\ \mu$  high,  $1.5-3\ \mu$  apart; muri do not extend to central portion of either surface; exine otherwise laevigate, total thickness  $2\ \mu$ .

*Remarks.* This distinctive, alete species, characterized by simple, radially disposed muri, has not been recorded in available literature. It shows considerable size variation, but is otherwise morphographically constant. *R. costatus* sp. nov. occurs in many of the Spitsbergen Lower Carboniferous samples, but is always a minor constituent.

## INCERTAE SEDIS

## Genus SPINOZONOTRILETES Hacquebard 1957

*Type species.* *S. uncatus* Hacquebard 1957.

*Discussion.* This and several other genera were instituted by Hacquebard (1957, pp. 314-15) as convenient subdivisions of the broad subgroup *Archaeozonotriletes* Naumova 1953. Both Naumova and Hacquebard used the term 'perispore' to denote the usually strongly developed, often conspicuously sculptured outer membrane which encloses and frequently almost obscures the central body of many of the spores embraced by the subgroup. It is, however, highly questionable whether a true perispore (perine), as usually understood (cf. Erdtman 1952; Harris 1955), is represented.

Potonié (1960, p. 42) suggested that the 'central body' seen in *Spinozonotriletes* may be a mesospore, a feature which, according to Potonié (1958, p. 21), is present also in the type species of *Grandispora* Hoffmeister, Staplin, and Malloy 1955.

From text-figs. 5, 6c of Richardson (1960) it is evident that his genus *Ancyrospora* shows wall features similar to those of *Spinozonotriletes*. Richardson (p. 55) applied the term 'bladder' to the thick, strongly sculptured, outer membrane (which he regarded as the exoexine) enveloping the central body (intexine), and thus assigned *Ancyrospora* to the Monosaccites. There seems to be considerable doubt, however, as to whether the outer enveloping layer of the exine in these spores is truly comparable to the exoexine (bladder) of typical Palaeozoic monosaccate types (e.g. *Endosporites*, *Remysporites*, *Velosporites*). Thus until further work is done on the structure of such forms as *Spinozonotriletes*, their non-committal suprageneric assignment seems preferable.

*Grandispora* was described by Hoffmeister, Staplin, and Malloy (1955) as possessing a 'central body wall only slightly thicker than the bladder wall', a feature which together with its constantly subcircular amb permits clear discrimination from *Spinozonotriletes*.

*Affinity*. Unknown.

*Spinozonotriletes uncatus* Hacquebard 1957

Plate 94, figs. 4-6

*Description of specimens*. Spores radial, trilete; amb convexly subtriangular. Laesurae with prominent, folded, flange-like lips (up to  $5\ \mu$  wide and  $7\ \mu$  high) extending to equator. Exoexine conspicuously sculptured with large, simple spines which are particularly frequent around the equatorial regions, less abundant in the polar areas; some specimens were noted in which the spines were reduced or absent on finely granulate contact areas. Spines have broad, circular bases ( $2-6\ \mu$  wide) which often appear rather bulbous in lateral view; length  $4-19\ \mu$ . This wide variation in spine dimensions is between specimens rather than within specimens, which individually bear spines of markedly uniform size. Exoexine thickness  $3-5.5\ \mu$  (exclusive of spines); commonly folded. Intexine rather indistinct, more or less conformable with equatorial outline, diameter roughly three-quarters overall diameter.

*Dimensions* (66 specimens). Overall equatorial diameter (exclusive of spines)  $74-150\ \mu$  (mean  $104\ \mu$ ). This is closely conformable with the size range stated by Hacquebard (1957, p. 316).

*Comparison*. *Spinozonotriletes uncatus* may be conspecific with *Acanthozonotriletes senticosus* Ishchenko 1956 (p. 87; pl. 16, fig. 200), which is somewhat smaller ( $67-70\ \mu$ ), but is otherwise very similar.

*Previous records*. From the Horton group (lowermost Mississippian) of Nova Scotia, Canada (Hacquebard 1957). The possibly identical species *Acanthozonotriletes senticosus* is confined to Tournaisian strata of the western Donetz Basin (Ishchenko 1956).

*Spinozonotriletes balteatus* sp. nov.

Plate 95, figs. 4-6; text-fig. 11b

*Diagnosis*. Spores radial, trilete; amb roundly subtriangular to oval. Laesurae obscured by elevated, narrow, membranous, flange-like lips, frequently contorted due to compression and extending to limbate equatorial margin. Intexine indistinct to perceptible, roundly subtriangular. Distal surface of exoexine densely and uniformly sculptured with small, simple spinae which sometimes coalesce to form a rugulate pattern; spines usually evident at equator, sparsely scattered to absent on proximal surface. Spines have rounded to polygonal bases (diameter  $0.5-2.5\ \mu$ ); length  $1-2\ \mu$ . Equatorial margin of exoexine marked by well-defined limbus  $3.5-7\ \mu$  broad in polar view.

*Dimensions* (40 specimens). Overall equatorial diameter  $51-102\ \mu$  (mean  $73\ \mu$ ); diameter prescribed by intexine  $30-59\ \mu$  (mean  $42\ \mu$ ).

*Holotype*. Preparation P149A/3, 30.5 97.5. L.1241.

*Locus typicus*. Triungen (sample G1470), Spitsbergen; Lower Carboniferous.



*Description.* Holotype 77  $\mu$  overall, irregularly roundly subtriangular; sinuous laesurate lips extend to conspicuously limbate margin; intexine perceptible, 44  $\mu$  in diameter; distal surface of exoexine covered with small, crowded spinae which are often coalescent at their bases; apart from spines, exoexine laevigate. Obliquely compressed specimens common; in such cases the limbus appears as a well-defined, dark, transgressive band, marking the true equatorial margin.

*Remarks.* This species, characterized by the presence of a limbus and of predominantly distal spinose sculpture, appears unparalleled in available literature. On the basis of its exoexinal sculpture and somewhat obscure intexine, the species finds suitable inclusion within *Spinozonotriletes* Hacquebard.

#### Genus TETRAPORINA Naumova 1939 ex Naumova 1950

*Type species.* *T. antiqua* Naumova 1950 (designated by Potonié 1960, p. 130).

*Discussion.* This genus, recently validated by Potonié (1960), was instituted by Naumova (1939, p. 357) as a subgroup of her group *Tetraporosa*, which she included within the class *Porosa* Naumova. The original diagnosis of *Tetraporina* stated 'pollen with four pores, without folds', and according to Naumova the class *Porosa* 'belongs exclusively to the *Angiospermae*'. Subsequently, Naumova (1950) and Teteriuk (1956) have described a number of Russian Lower Carboniferous species of *Tetraporina*, and reaffirmed their belief in the angiospermous affinity of such forms. More recently, the names *Azonotetraporina* and *Zonotetraporina* were introduced by Teteriuk (1958, pl. 1 explanation) merely as captions to some drawings of further Lower Carboniferous *Tetraporina*-like spores, and must therefore at this stage be considered *nomina nuda*. Thus Staplin's (1960, p. 6) usage of *Azonotetraporina* as a valid generic entity is unacceptable. Furthermore, from the figures given by Teteriuk (1958) it seems likely that the forms were differentiated only on the basis of wall thickness.

*Tetraporina* Naumova is rather an unsatisfactory taxon in that the supposedly diagnostic four 'pores' are often either incompletely or not developed; this is apparent from both Naumova's and Teteriuk's illustrations and also from the Spitsbergen specimens described below. These latter represent an interesting new Lower Carboniferous occurrence, but are insufficient basis for the seemingly necessary, comprehensive reappraisal of the genus, the most significant feature of which appears to be constantly quadrangular shape.

*Affinity.* The angiospermous attribution (Naumova 1939, 1950; Teteriuk 1956, 1958) of *Tetraporina* has been regarded doubtfully by many subsequent authors (Staplin 1960, p. 6; Scott, Barghoorn, and Leopold 1960, p. 287; Hughes 1961, p. 89). Certainly the brief descriptions and line drawings of the Russian forms are inadequate for a critical assessment of botanical affinity. The possible algal affinity of the genus was discussed recently by Scott *et al.* (1960, p. 287), who noted its close morphological similarity with species of the unicellular green alga *Tetraëdron*. Valuable support in this connexion is apparent from a paper by Churchill (1960), who figured a number of Cainozoic and living unicellular algae and aplanospores; of his illustrations, fig. 1, nos. 3, 4, 6, 8, 11, 12, and 13 show striking superficial resemblance to *Tetraporina*. Moreover, Dr. Churchill

has kindly examined the specimens described below and he considers that there is little doubt of their algal affinity.

*Tetraporina incrassata* Naumova 1950

Plate 95, figs. 12, 13

*Description of specimens.* Spores alete; outline quadrangular with distinctly concave sides and rounded corners. Exine scabrate to almost smooth, generally about  $2\ \mu$  thick; locally  $\pm$  conspicuously thickened at corners, which may occasionally show aperture-like perforations.

*Dimensions* (12 specimens). Diagonal length 46–70  $\mu$  (mean 60  $\mu$ ).

*Previous records.* From the Lower Carboniferous of the Moscow Basin (Naumova 1950).

*Tetraporina glabra* Naumova 1950

Plate 95, fig. 11

*Description of specimens.* Spores alete; outline quadrangular with concave sides and rounded angles. Exine uniformly thick (3  $\mu$ ), laevigate. In the figured specimen one minute perforation is present in the vicinity of each corner; the other specimens encountered appear non-perforate.

*Dimensions* (3 specimens). Diagonal length 50–54  $\mu$ .

*Previous records.* From Lower Carboniferous deposits of the Moscow Basin (Naumova 1950).

*Tetraporina horologia* (Staplin) comb. nov.

Plate 95, figs. 14, 15

1960 *Azonotetraporina?* *horologia* Staplin p. 6; pl. 1, figs. 4, 6.

*Description of specimens.* Spores alete; outline quadrangular with concave to almost straight sides and rounded corners. Exine thin, hence readily folded and distorted; surface finely granulate to slightly roughened. Apertures rarely evident, but often simulated by arcuate folds at the corners.

*Dimensions* (14 specimens). Diagonal length 44–71  $\mu$  (mean 56  $\mu$ ).

*Remarks.* As discussed above, *Azonotetraporina* Teteriuk is not a valid genus and in any case appears to be a misconceived subdivision of *Tetraporina* Naumova. Accordingly Staplin's species, which was questionably referred to *Azonotetraporina*, is here transferred to *Tetraporina*.

*Comparison.* *Tetraporina glabra* Naumova 1950 (pl. 1, figs. 5, 28) is thicker-walled, but otherwise similar to *T. horologia* (Staplin) comb. nov.

*Previous records.* From the Golata formation (Upper Mississippian) of Alberta, Canada (Staplin 1960).

# MICROFLORAL ASSEMBLAGES AND STRATIGRAPHICAL APPLICATIONS

The primary object of this section is to assess the stratigraphical significance of the microfloral elements, described above, of the Lower Carboniferous succession of Spitsbergen. It will be shown below that two distinct, successive, microfloral suites (assemblages) are distinguishable, each characterized by a number of distinctive microspore species of restricted stratigraphical ranges and hence of considerable correlative value both within and outside Spitsbergen. Evidence will be adduced as to the age of these assemblages, with reference to the standard European stage subdivisions of the Carboniferous, on the admittedly indirect basis of Russian and North American microfloral parallelism.

As noted previously, the microfloras examined in the present study have been recovered from a wide variety of lithologies (especially clastic rock types), and are thus probably fairly representative of the overall contemporary flora. Collecting has been insufficiently detailed, however, to permit palaeoecological inferences based upon quantitative/qualitative studies of the microflora observed throughout a limited stratigraphical succession (cf. Neves 1958).

## *Delineation of microfloral assemblages*

Detailed study of microfloras contained in samples collected from the three successions, at Birger Johnsonfjellet, Triungen, and Citadellet (see text-fig. 2), has given an overall picture, as comprehensive as sampling intervals permit, of the microfloral succession in the Spitsbergen Lower Carboniferous. Tables 1 and 2 list all the microspore species present in the samples from these localities; in the preparations of most samples, abundance and sufficiently good preservation of the microfloral elements has permitted representation on a quantitative basis, resulting from a count of 250 specimens per sample. It will be evident from these Tables that, whilst many species are ubiquitous, a fairly large number possess restricted vertical distribution. A more or less uniform microfloral suite occurs in samples from the lower parts of the Birger Johnsonfjellet and Triungen sections and in the entire collected Citadellet section (see Table 1). This distinctive suite is here conveniently designated as the *Rarituberculatus* Assemblage. The

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## EXPLANATION OF PLATE 95

All figures  $\times 500$ , and from unretouched negatives.

Figs. 1–3. *Retialetes radforthii* Staplin 1960. 1, Preparation P155/7, 36·0 106·0 (L.1246). 2, Showing longitudinal rupture; preparation P155/13, 33·9 105·2 (L.1247). 3, Preparation P155/10, 36·9 103·3 (L.1248).

Figs. 4–6. *Spinozonotriletes balteatus* sp. nov. 4, Holotype; distal surface. 5, Tetrad; preparation P149A/1, 26·4 100·4 (L.1243). 6, Proximal surface; preparation P145B/1, 17·9 95·6 (L.1242).

Figs. 7–9. *Radialetes costatus* gen. et sp. nov. 7, Preparation P163/1, 38·7 107·9 (L.1250). 8, Preparation P145B/7, 35·2 106·0 (L.1251). 9, Holotype.

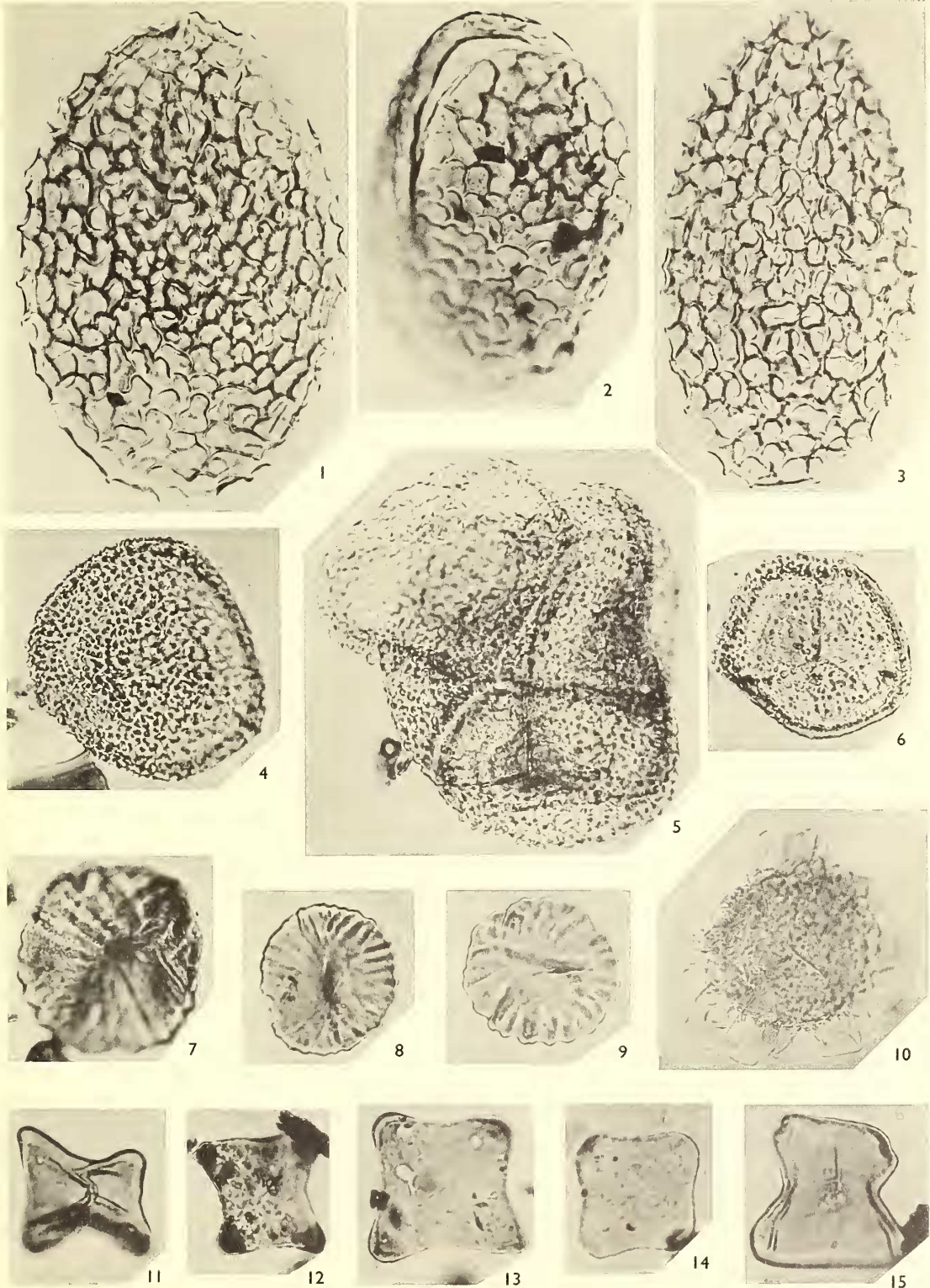
Fig. 10. *Alatisporites tessellatus* Staplin 1960. Proximal surface; preparation P163/2, 40·4 113·5 (L. 1245).

Fig. 11. *Tetraporina glabra* Naumova 1950. Preparation P145B/5, 35·5 104·2 (L.1255).

Figs. 12, 13. *Tetraporina incrassata* Naumova 1950. 12, Preparation P139/4, 30·1 103·6 (L.1253). 13, Preparation P145A/1, 44·7 102·6 (L.1254).

Figs. 14, 15. *Tetraporina horologia* (Staplin) comb. nov. 14, Preparation P181/3, 32·1 105·5 (L.1256). 15, Preparation P202/3, 31·9 97·7 (L.1257).





PLAYFORD, Lower Carboniferous microspores





microspore species	BIRGER JOHNSONFJELLET						TRIUNGEN		CITADELLET					
	G1086	G1087	G1088	G1089	G1090	G1091	G1473	G1472	G1445	G1446	G1448	G1450	G1451	G1453
<i>Chaetosphaerites pollenisimilis</i>								x						
<i>Leiotriletes inermis</i>	x	2.0	0.4	x	x	3.6	1.2	2.4	4.4	1.6	4.4	5.2	2.4	4.4
<i>L. subintortus</i> var. <i>rotundatus</i>		x	1.6	2.8	x	x	x	x	x	1.2	2.0	2.0	1.6	4.4
<i>L. ornatus</i>	x		x	0.4	x	1.6		x	0.8	0.4	0.8	1.6	0.8	1.6
<i>L. microgranulatus</i>							x				x	0.8	0.8	4.0
<i>Punctatisporites glaber</i>	x	3.6	2.8	2.8	x	3.6	0.4	1.6	5.6	6.4	7.2	10.0	5.6	8.8
<i>P. parviverruculatus</i>				2.0		1.6		x	0.4	0.4	x	2.0	0.8	0.8
<i>P. labiatus</i>				0.4				x	x		0.4	1.6		
<i>P. pseudobeus</i>								0.4						
<i>Calamospira microrugosa</i>	x	2.4	2.0	1.2		0.8	1.2	0.8	3.2	2.8	3.6	3.2	4.0	2.8
<i>Phyllotheotrilletes rigidus</i>			x			x			1.2		0.8	x	2.8	2.8
<i>Granulatisporites planiuculus</i>	x													
<i>Cyclogranisporites lasius</i>	x	2.4	0.4			0.4		0.4	3.2	1.6	5.6	5.2	2.8	2.4
<i>C. flexuosus</i>								0.8	x	0.8	0.8	1.6	0.8	1.2
<i>Verrucosiporites gobbettii</i>				x	x			x			0.4	1.2	1.2	1.2
<i>Lophotriletes confusus</i>						x			4.4	1.2	x	0.4	x	x
<i>Apiculatisporia macrurus</i>				0.4			3.2	0.4			0.4	0.8		
<i>Acanthotriletes multisetus</i>				x				0.8	2.4	11.2	12.0	6.4	5.2	4.8
<i>A. mirus</i>								x			x			
<i>Convolutispora tuberculata</i>				3.6	x	0.4	0.8	0.8	1.6	1.2	4.4	2.8	1.6	
<i>C. vermiformis</i>	x	4.8	0.4	2.0			6.8	0.4	3.6	3.2	1.6	1.6	0.8	0.4
<i>C. harlandii</i>		3.2	0.8	2.0	x	1.2		2.8	0.4	0.8	0.4	0.4	1.6	0.4
<i>C. crassa</i>				0.4		0.4		0.4	x	x	x	0.8	x	
<i>Microreticulatisporites lunatus</i>				0.8		0.4	0.8	0.4		1.6	2.8	2.0	0.8	
<i>Dictyotriletes caperatus</i>			x	0.4				2.8	0.8	1.2	0.8			
<i>Reticulatisporites cancellatus</i>			0.8	4.8	x	0.8		12.8	0.8	0.8	0.8	x	2.8	1.2
<i>P. planus</i>		0.4	0.4	0.8	x	x		0.4	0.8	0.4	x			
<i>Perotriletes perinatus</i>		2.0	x	1.2	x	0.4	0.4	x	1.2	1.6	1.2	1.2	0.4	0.4
<i>P. magnus</i>	x	4.4	0.4	x			0.8	0.4	x	3.2	x	x	x	0.8
<i>Triquitrites batillatus</i>					x	1.6								
<i>Tripartites incisotrilobus</i>				19.2	x	2.8		2.8			0.4	1.2	2.8	7.6
<i>Stenozonotriletes stenozonalis</i>			x	0.4		x	x	x	x	x	x			
<i>S. facillis</i> var. <i>praecrassus</i>							x	2.4	0.8	0.4				
<i>S. simplex</i>	x	2.0	3.2	x			1.6	x	0.8	1.6				
<i>S. inductus</i>	x	x					x	x	x	0.4				
<i>S. clausus</i>	x			0.8			0.4	0.8	0.4	0.4				
<i>S. perforatus</i>				x		x	2.0	0.8	0.8	2.0				
<i>S. cf. spetecandus</i>								x	x		x	x	x	
<i>Mucrospora intorta</i>	x					x			x	x				
<i>M. conpuplicata</i>		2.0		3.6		1.6		0.8	x	0.4	4.4	x	1.6	1.6
<i>M. sublobata</i>				x		x		0.8			2.0	0.8	0.8	0.8
<i>Anulatisporites anulatus</i>				x	x	6.4	10.8	x	x	5.2	2.4	3.2	2.4	
<i>A. labiatus</i>			3.2	3.2	x	1.6	3.6	8.0	18.8	8.4	2.8	0.4	5.2	0.8
<i>A. orbiculatus</i>								x	0.8	0.4	x	x	x	
<i>A. canaliculatus</i>			0.8	x	x	x	x	0.8	0.4	1.2	0.8	0.8	x	x
<i>Densosporites dentatus</i>				2.4	x	36.0	30.4	1.6			4.0	4.8	6.4	4.8
<i>D. intermedius</i>				2.8	x	3.2		0.4			0.8	1.2	5.0	6.4
<i>D. variabilis</i>				x				1.2					3.2	3.2
<i>D. striatiferus</i>		21.2							x	0.4				
<i>D. spitsbergensis</i>			2.8	4.0	x	8.0		1.6			3.6	3.6	5.6	
<i>D. variomarginatus</i>			8.4	16.8	x	4.8		10.8		1.2	10.0	6.4	16.8	10.8
<i>Labiadensites fimbriatus</i>				1.2				0.4					x	0.4
<i>Knoxisporites cinctus</i>						x			1.6	0.8	x	x	x	x
<i>K. margarethae</i>		0.8		0.8		0.8	0.4	x	2.8	6.0	x	x	x	x
<i>K. literatus</i>				1.6		1.6		0.4	0.4		0.4	0.4	0.4	0.8
<i>K. hederatus</i>				x				x			0.4	0.8	0.8	0.8
<i>Cristatisporites echinatus</i>								x				x	x	x
<i>Lophozonotriletes rarituberculatus</i>	x	7.2	1.2	2.8	x	0.8	0.4	x	4.4	2.8	0.8	0.8	0.8	0.8
<i>L. dentatus</i>		1.2				x			1.6					
<i>L. variverrucatus</i>	x							0.4	1.2	2.4	x	0.4	0.4	x
<i>Tholisporites foveolatus</i>		3.6	43.6	2.4			14.8	26.0	18.4	22.0	2.0	0.8	0.8	
<i>Endosporites micromanifestus</i>			0.4	0.4		x		x	0.8	0.8	4.4	5.2	1.2	2.4
<i>Velosporites echinatus</i>			0.4	0.4	0.8		0.4	6.0	x	x	0.8	0.4	x	x
<i>V. microreticulatus</i>				0.4				x			x	x		
<i>Spinizonotriletes uncutus</i>				x			0.4	1.2		x	x	1.2	0.4	1.2
<i>Alatisporites tessellatus</i>				0.4										x
<i>Radiales costatus</i>			0.4	x			x	x	x	0.8	0.4		x	0.4
<i>Tetraporina incrassata</i>						x								
<i>T. horologia</i>														x

TABLE 1. Microspore distribution in samples from the Citadellet succession and from the lower parts of the sections exposed at Birger Johnsonfjellet and Triungen. In most samples, constituent species are recorded as percentages, which are based upon individual counts of 250 specimens. Indeterminable specimens in each case comprise the percentage complementary to that of specifically determinable specimens. 'x' indicates observed presence in a particular sample, but not in actual count. Relatively sparse and poorly preserved spores were recovered from samples G1086 and G1090, and hence neither was considered suitable for quantitative specific estimation. Correction: for *Densosporites intermedius* read *D. diatretus* (see p. 623).

microspore species	BIRGER JOHNSONFJELLET									TRIUNGEN					
	G1092	G1093	G1095	G1096	G1098	G1099	G1101	G1102	G1471	G1470	G1469	G1468	G1467	G1466	G1465
<i>Chaetosphaerites pollenisimilis</i>	0.4	1.2		2.4	1.2	x		0.4		0.4			x	3.6	
<i>Leiotrilites inermis</i>	1.6	0.8	1.6	2.4	2.0	x		0.8		0.8	x	x	1.6	0.4	x
<i>L. subintortus</i> var. <i>rotundatus</i>	0.4	x	1.6	1.2		x	x	1.6	x	0.4		x	0.4	0.4	
<i>L. ornatus</i>					x			0.4	x			0.4	x	0.4	
<i>L. curiosus</i>										0.8				x	
<i>Punctatisporites glaber</i>	0.8	0.4	1.2	3.2	1.2	x		2.4	x	5.6	x	1.2	2.0	0.8	
<i>P. parvivermiculatus</i>			1.6										2.0		
<i>P. pseudobesius</i>	1.2	0.4	x	0.4						4.8			x	2.0	
<i>P. stabilis</i>															
<i>Calamospora microrugosa</i>	0.8	0.4	0.8	2.4	0.4		x	0.4	x	2.8		2.0	2.4	1.2	
<i>Phyllotheconitrites rigidus</i>	x	x	x		x	x		x	x	0.4		x	0.4	x	
<i>Waltzispora lobophora</i>				x	x			x		x			x	0.4	
<i>W. albertensis</i>								0.8					x	6.4	
<i>W. sagittata</i>								x							
<i>Cyclogranisporites lasius</i>	x	x		0.8							x	5.2	0.8	x	
<i>C. flexuosus</i>	x		0.4		x	x		0.4						x	
<i>Verrucosporites eximius</i>					x	x	x			0.8			0.4	x	
<i>Anapiculatisporites concinnus</i>			0.4					1.2		0.8				8.8	
<i>A. serratus</i>										1.2	x			2.4	
<i>Acanthotrilites multisetus</i>												0.4			
<i>Hystricosporites</i> sp.			x												
<i>Convolutispora tuberculata</i>	x		2.0		x		x		x	0.4	x	36.0	2.4	x	
<i>C. clavata</i>												0.8	x		
<i>C. harlandii</i>	2.0	0.4	0.8												
<i>C. crassa</i>	x	x													
<i>C. labiata</i>	0.4			0.4	x					0.8	x				
<i>C. usitata</i>	1.2												x		
<i>Microreticulatisporites lunatus</i>	x		0.4		x					x	x				
<i>Reticulatisporites rudis</i>										x				x	
<i>R. cancellatus</i>	4.4	2.0	2.8	2.4	0.4	x		2.0		0.8	x	x	x	0.4	
<i>R. variolatus</i>	1.6		0.8		x			x		0.4	x	x	x	x	
<i>R. peltatus</i>			x	1.6	x		x	x	x	0.4			x	x	
<i>R.?</i> sp.														x	
<i>Foveosporites insculptus</i>			0.4		0.4	x		x	x	4.4	x	0.8	4.0	x	
<i>Perotrilites perinatus</i>	x		x						x						
<i>P. magnus</i>	x	0.4	0.8						x	x					
<i>Triquitrites trivalvis</i>					0.8	x	x	0.8						0.4	
<i>T. batillatus</i>	5.6	1.2	0.8	0.4	x					0.4			0.4	x	
<i>Tripartites incisotrilobus</i>	1.2		0.4		2.8	x	x	0.8		0.8		1.2	0.8	1.2	
<i>T. complanatus</i>					x			x		x				0.4	
<i>Stenozonotrilites clarus</i>	x		x				x		x				0.4	0.4	
<i>S. facilis</i> var. <i>praecrassus</i>	0.4									x				x	
<i>S. perforatus</i>		0.4											x		
<i>S. cf. spetandus</i>			x												
<i>Murospora intorta</i>	0.8	0.4	0.4	0.4	0.8	x	x	0.8	x	x			x	0.8	
<i>M. aurita</i>	12.8	24.8	4.8	28.0	4.4	x	x	7.2	x	1.2		0.4	0.4	5.2	x
<i>M. conduplicata</i>	x	0.4	1.2	0.4	x	x	x	0.4	x	0.4	x	0.8	0.4	2.0	x
<i>M. sublobata</i>	0.4		x		0.4	x	x	x	x	0.4		x	x	1.2	x
<i>M. dupla</i>															
<i>M. strigata</i>					x									0.4	
<i>M. tripulvinata</i>					x										
<i>M. friendii</i>		2.0			x	x		x		0.4		0.4		0.4	
<i>Anulatisporites anulatus</i>	1.2	0.8	4.8	2.0	0.4	x		0.4	x	2.0		1.2	4.0	0.8	
<i>A. labiatus</i>	1.6	0.4	0.4		x	x	x		x	0.4	x	0.8	x		
<i>Densosporites bialatus</i>			18.4	1.6	0.8	x		1.2	x	x		0.8	0.8	1.2	
<i>D. dentatus</i>	3.2	2.0	12.0	2.0	4.0	x		4.0	x	8.4	x	0.8	12.4	1.2	
<i>D. subcrenatus</i>					x	x	x	x	x	x	x	x	0.4	0.8	
<i>D. intermedius</i>	3.6	6.8	4.2	1.2				0.4	x	3.6	x		2.0	1.2	
<i>D. variabilis</i>	26.4	23.6	16.8	6.4	4.0	x	x	1.6	x	12.8	x	0.8	46.0	6.4	
<i>D. duplicatus</i>			0.4		0.8			0.4	x	x		0.8	x	x	
<i>D. spitzbergensis</i>	10.0	13.2	3.6	2.0						1.2	x		0.8	2.4	
<i>D. rarispinosus</i>					0.8			4.4	x	x	x				
<i>D. aculeatus</i>			2.4	x		x		x	x	0.8	x		0.8		
<i>D. sp.</i>					x							x			
<i>Labidensites fimbriatus</i>	5.6	0.8	0.8	x	0.4	x	x	x	x	x		6.4	2.0	0.4	
<i>Knoxisporites cinctus</i>			1.2												
<i>K. margarethae</i>	x														
<i>K. literatus</i>	6.4	11.2	2.4		x	x	x	0.8			x	0.4		0.4	
<i>Lycospora uber</i>			2.0	56.8	43.2	x	x	61.2	x	5.6	x	2.4	2.4	32.4	
<i>Lophozonotrilites appendicea</i>								x		0.4	x		0.4	1.6	
<i>Monilospora triungensis</i>														0.4	
<i>M. dignata</i>								x						0.8	
<i>Potoniesporites delicatus</i>			x		1.2	x		0.4		x			0.4	x	
<i>Cirratiradites solaris</i>								x						x	
<i>C. elegans</i>	x		0.8	x						0.4					
<i>Camptozonotrilites velatus</i>	2.4	0.4	2.0					x	x	1.6	x	0.4	1.2	x	
<i>Diatomozonotrilites saetosus</i>			x		1.6	x	x	0.4					0.8	x	
<i>D. hughesii</i>			x	x		x	x	0.8	x	6.0		0.8	0.8	2.4	
<i>D. trilinearis</i>										4.0		4.4	0.8	0.4	
<i>D. rarus</i>									x					x	
<i>Endosporites micromanifestus</i>	x		0.4	x	x	x	x	0.4						x	
<i>Remysporites albertensis</i>										x			x		
<i>Velosporites microreticulatus</i>	x														
<i>Spinozonotrilites balteatus</i>										13.6	x	21.6	0.8	2.8	
<i>Alatisporites tessellatus</i>				0.4				x							
<i>Retialetes radforthii</i>							x							x	
<i>Radialetes costatus</i>		1.2	0.4						x	x			0.4	x	x
<i>Tetraporina incrassata</i>														x	
<i>T. glabra</i>														x	
<i>T. horologia</i>										x				0.4	x

TABLE 2. Microspore distribution in Birger Johnsonfjellet and Triungen samples succeeding those documented in Table 1. In most samples, constituent species are recorded as percentages, which are based upon individual counts of 250 specimens. Indeterminable specimens in each case comprise the percentage complementary to that of specifically determinable specimens. 'x' indicates observed presence in a particular sample, but not in actual count. Counting was precluded in samples G1099, G1101, G1471, G1469, and G1465, owing to sparse occurrence and/or poor preservation of the recovered spores. Correction: for *Densosporites intermedius* read *D. diatretus* (see p. 623).